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Long-term effects of habitat and management changes on steelhead production: results from an individual-based model

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Long-term effects of habitat and management changes on steelhead production: results from an individual-based model

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Abstract

Steelhead populations support an economically valuable fishery in the Great Lakes region. Development of the region, resulting in land use changes and the introduction of hydropower, has affected the riverine habitat used by steelhead. I have developed an individual-based model of steelhead in the Manistee River, Michigan that simulates the long-term production of steelhead from the river. The model begins each year with a spawning population that produces redds for that year and then follows the offspring from each redd as individuals until they smolt one, two, or three years after spawning. Simulations run for ten-year periods. The simulated individuals are subjected to mortality from predation, starvation, and temperature extremes. Predation is a length-based mortality and is thereby affected by growth. Growth is determined by an individual's foraging success and bioenergetics. I conducted simulation experiments to examine the effect of changes in spawning numbers, temperature, and flow regime, on the number of individuals smolting in the river each year. Simulations reveal that the current flow regime and colder water temperatures are most beneficial for steelhead production and increasing the number of spawners does not increase steelhead production. The results also suggest that the young-of-the-year (YOY) stages have the greatest impact on steelhead production because the model showed no indication that steelhead life stages older than the YOY could compensate for density-related losses that occurred during the first year.

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LONG-TERM EFFECTS OF HABITAT AND MANAGEMENT CHANGES ON STEELHEAD PRODUCTION: RESULTS FROM AN INDIVIDUAL-BASED MODEL

Introduction

Fish are exploited around the globe for their nutritional and economic value. Unfortunately, natural and anthropogenic factors have created unsuitable environments where fish populations can no longer thrive. As the actual importance of fish and fisheries for the economy has been recognized, there has been a rise in resources devoted to fisheries studies (Ormerod, 2003). Models have been developed to help explore solutions to problems that laboratory and field studies cannot accomplish alone (Swartzmann, 1987; DeAngelis et al., 1990; Tyler & Rose, 1994; Giske et al., 1998) and are a practical way to determine how ecological factors affect different populations. Individual-based models (IBMs) are unique in their ability to examine some critical questions in the area of population dynamics (Huston et al., 1988; DeAngelis et al., 1990). In this work, I developed an extension of an existing IBM for steelhead populations in the Manistee River, MI and used it to investigate the effects of changes in environmental factors and spawning population densities on steelhead recruitment in the Manistee River, MI.

Steelhead (*Oncorhyncus mykiss*), from the Salmonidae family (commonly referred to as the salmonids), were introduced into the Great Lakes in 1876 (Thompson, 2004). They are native to the Pacific Coast but have been transplanted to many different regions in North America. The Great Lakes are one of the regions that has benefited economically from the introduction of salmonids; it is estimated that recreational fishing

for steelhead generates $1 billion annually (Jakubiak, 1999). Since their introduction, steelhead have become the main catch in Michigan's sport fishery (Woldt & Rutherford, 2002) and many studies have focused on improving the future of the steelhead population. However, steelhead are not immune to natural or anthropogenic changes to the environment. One of their first population declines came with the introduction of hydroelectric dams on Lake Michigan tributaries (Woldt & Rutherford, 2002).

In general, dams have severely altered river ecosystems by affecting water temperature, flow regimes, sediment transport, fish migration, and drift of aquatic invertebrates (Babbitt, 2002; Poff & Hart, 2002; Woldt & Rutherford, 2002; Horne et al., 2004; Lytle & Poff, 2004). The adverse effects of dams have led people to believe dam removal will restore a river's ecosystem (Hart et al., 2002; Doyle et al., 2003), but the potential dangers (e.g., sediment build-up, changes to flow and temperature regimes) of removing and modifying dams have been questioned and studied by many (Babbitt, 2002; Osmundson et al., 2002; Horne et al., 2004). In this study, my model simulates changes to the environment that may result from modifications of dam operation and how the steelhead population in the Manistee River may respond to such changes. Specifically, dam operations can be altered to affect water temperature and water discharge levels and the simulation experiments performed within this thesis focus on these environmental changes.

Water temperature plays an important role in fisheries because it is linked to growth, bioenergetic rates, food availability, drift foraging, movement, spawning time, development, survival, recruitment, and mortality (Giske et al., 1998; Van Winkel et al., 1998; Railsback & Rose, 1999; Workman et al., 2002). The location of the dam's

withdrawal, top or bottom of the water column, can release water with varying temperatures. The thermal regime of the reservoir determines the water temperature that will be discharged from the dam. If a thermocline exists in the reservoir the river may benefit from a temperature decrease associated with bottom withdrawal, if no thermocline exists the withdrawal location may not affect downstream temperatures (Horne et al., 2004).

The flow of a river, much like temperature, can affect the growth, development, survival, recruitment, and mortality of fish (Poff et al., 1997; Van Winkel et al., 1998; Horne et al., 2004). Flow alters the depth and velocity of the river and the duration, seasonal timing, frequency, and magnitude of different flow events determine the extent to which organisms will be affected (Poff et al., 1997; Hart et al., 2002; Covington & Hubert, 2003; Lytle & Poff, 2004). Dams control the amount of water discharged from the reservoir and can manage the downstream flow. Two major types of flow management are employed by dam operators: peak and run-of-river. Peak flow management periodically releases large amounts of water, creating an abnormal and harsh environment for river occupants (Poff et al., 1997; Woldt & Rutherford, 2002). Run-of-river management, on the other hand, allows the water to flow naturally (Poff & Hart, 2002), creating a more suitable environment for aquatic organisms.

Temperature and water discharge are two environmental factors that can be altered in the Manistee River since there are two dams on the river. I focused my study on the effects of Tippy Dam, the dam closest to the mouth of the river. In 1998, the flow regime of Tippy Dam was changed from peak to run-of-river flow (Woldt & Rutherford, 2002), although it is still possible for dam operators to make further modifications to the flow

regime. Tippy Dam is also a top-withdrawal dam, increasing downstream water temperatures during the summer months (Horne et al., 2004).

Aside from temperature and discharge, my model also explores effects of stocking densities of spawning females on smolt production in the Manistee River by altering the number of spawning females. Even though there are naturally reproducing steelhead populations in the Great Lakes, the steelhead fishery is supplemented by annual stockings that help maintain the population (Woldt & Rutherford, 2002; Horne et al., 2004). The number of individuals that are stocked in a river can be critical to a population and to the success of stocking. When stocking a river, density-dependence may need to be taken into consideration since density-dependence can affect growth rate, mortality, and recruitment (Cowan et al., 2000). If survival and reproduction become limited by the amount of resources in the environment, increasing stocking populations will not increase recruitment. This model examines how stocking and the associated density-dependence may affect steelhead production.

The model presented in this thesis is an extension of the young-of-the-year (YOY) steelhead individual-based model constructed by Tyler & Rutherford (*in review*). The YOY steelhead IBM follows the steelhead life cycle for one year, from spawning until the end of the growing season (Day 275, October 2). My model is a multi-year model that tracks the individuals from the end of the growing season (Day 275) until they reach the appropriate size to smolt from the river. The new model runs for ten years simulating individuals from spawning to smolting.

Steelhead can reside in their natal river for up to three years until they are ready to migrate out of the river to join the adult population (Woldt & Rutherford, 2002; Myrick

& Cech, 2004). The three years steelhead can spend in the river is a substantial length of time for a life stage when compared with its previous life stages that can last from days to months. The importance of the three year period is not explored in the YOY steelhead IBM. My new model may help determine the importance of the post-YOY life stage in the river.

The model simulates the area downstream of Tippy Dam and subjects the population to different factors that management has the ability to alter, such as changes in water temperature, discharge rates, and spawning population. With this model, I show how specific management decisions may affect steelhead recruitment by examining the population's weight, density, and number of smolts in the Manistee River over multiple years.

Model Description

The individual-based model presented here (referred to as the 'riverine steelhead IBM') focuses on the riverine stages of the steelhead life cycle from the end of the first year growing season until the fish smolt and begin their migration to open water and enter the adult population. This model is an extension of the young-of-the-year (YOY) steelhead model constructed by Tyler & Rutherford (*in review*) (referred to as the 'YOY steelhead IBM') that encompasses the steelhead life cycle from spawning until the end of the first year growing season (Day 275, October 2). The riverine steelhead IBM has many similarities with the YOY steelhead IBM with a few important exceptions. The riverine steelhead IBM simulates individuals that reside in the river for multiple years until they are ready to smolt. The need for the riverine steelhead IBM arises from the fact that steelhead spend from one to three years in the river prior to smolting (Myrick & Cech, 2004). A model that captures this period of the life cycle will be able to simulate the effect of environmental and management changes and assess how such changes affect the non-YOY, pre-smolt life stages of steelhead. My model simulates multiple years and tracks individuals as they live through multiple years until they either perish or smolt.

The riverine steelhead IBM has two distinct components, the model environment and the steelhead population. The model environment is a generic representation of the Manistee River where site-specific data were used to generate the environment, but simulated cells do not match exact locations on the river. The steelhead population is modeled after individuals from the Manistee River and the Great Lakes region in general, but further data had to be extrapolated from studies performed in western or southern rivers and laboratory experiments. In the riverine steelhead IBM, steelhead populations

experience realistic environmental conditions with altered prey densities, actual field water discharge levels, and the addition of age 1+ steelhead populations.

Model Environment

The riverine steelhead IBM has the ability to show how different environmental factors affect the population from year to year. To accomplish this, the model environment is reset on the first day of every year to ensure the current year will differ from the previous one. The model environment consists of 100 unique cells that alter the development and life history of steelhead in the model river. Each cell has a set of common and exclusive features. All of the cells share the same daily values for water temperature, stream discharge, daylight hours, and prey densities. Exclusive features such as cell dimensions (depth, width, distance), steelhead feeding stations, and substrate characteristics differ between cells and create the cell's individuality. Overall the model environment in the riverine steelhead IBM differs little from that developed for the YOY steelhead IBM. Here I summarize the model environment and pay specific attention to features that are unique to the riverine steelhead IBM.

Features common to all cells

Water temperature and daylight hours are features that do not change from the YOY steelhead IBM to the riverine steelhead IBM. Temperature is based on data collected at Tippy Dam from 1997-1998. A simulated mean temperature is calculated everyday and model temperatures are subject to daily deviations from the mean (Figure 1; See Tyler & Rutherford (*in review*) for detailed explanation on calculating deviations). Individuals are allowed to forage only during daylight hours (Tyler & Rutherford, *in*

review) which are calculated using 44.52 degrees latitude (Brock, 1981), the location of the Manistee River.

Prey densities in the riverine steelhead IBM follow a function that was fit to data from the Muskegon River, Michigan (Figure 2; Riseng & Wiley, unpublished data, University of Michigan, Jan. 25, 2006). The function used to simulate prey densities (equation 1), creates a temporal change in densities that rises in the spring and falls in the late summer and autumn.

$$PD = 0.0075 + \left(\frac{0.021}{1 + \exp\left(-\left(day - 320.5\right)/30\right)} \right) \cdot \left(1 - \left(\frac{1}{1 + \exp\left(-\left(day - 165.5\right)/15\right)} \right) \right) \quad (1)$$

Winter densities of drifting prey are low and this function assures that these densities do not differ during the winter season. This feature is critical because model simulations last multiple years and prey densities that show discontinuities at the beginning and ending of years may cause unreasonable results. This is a change from the prey density function used in the YOY steelhead IBM where discontinuous prey densities at the end of a year were unimportant because the model ended in the autumn.

The riverine steelhead IBM uses field data for the discharge rates (Figure 3). On the first day of a new year one of the 9-year daily discharge data sets (1990-1998) is randomly selected to be the daily discharge rates for that year (data from the USGS). Using field data can provide an accurate representation of the actual environment encountered in the Manistee River. I used this discharge approach in the riverine steelhead IBM to assure that discharge rates reasonably reflect the environment in the Manistee River.

Features varying among cells

Every cell has a set of features that are determined independently from other cells. Width, depth, distance, and water velocity all change relative to the water discharge ($m^3 \cdot s^{-1}$) from Tippy Dam. Using data from two transects of an IFIM study on the Manistee River (Ichthyological Associates, 1990), a relationship is derived linking the width and depth of each cell to water discharge. Each transect has its own set of parameters and a cell is randomly assigned one of the two transect parameter sets and random variation is then used to produce a 20% coefficient of variation in depth. The width of each cell (m) is determined directly from depth using a relationship derived from the same two IFIM transect data sets. The distance of a cell is determined by a random normal distribution with a 10% coefficient of variation from a mean of 50 m. The IFIM study provided only two transects in the high density spawning region of the Manistee River that this model environment is based upon.

Water velocity and substrate also differ for each of the 100 cells in the model environment. The water velocity is calculated by dividing the river discharge ($m^3 \cdot s^{-1}$) by the cross sectional area of the cell (m^2). Substrate is determined by the cell depth, water velocity, and random variation in local geology.

Each cell has a particular number of feeding stations that can be assigned to fry, parr, and yearling (parr age-1 and older) stages based upon the mean densities of each stage and where the stage feeds. The densities for feeding stations of fry, parr, and yearling are as follows: $100 \cdot m^{-2}$, $10 \cdot m^{-2}$, and $1 \cdot m^{-2}$, respectively (Grant & Noakes, 1987). Each stage also feeds in different areas of the river. Fry and parr are limited to feeding in the margins near the bank of the stream (within 1.5 m and 3.0 m of the river bank for fry

and parr, respectively) and yearling feed across the whole cell. The final number of feeding stations is the product of density and area for each life stage.

Steelhead Population

A simulation starts with a spawning female population and follows the offspring through egg, alevin, fry, and parr stages. Egg and alevin stages are modeled as cohorts, while the fry and parr stages are modeled as individuals. After the first simulation year, parr that have not died are allowed to stay in the river until they reach the smolting requirements. Throughout the rest of the paper age 1+ parr will be referred to as yearling.

YOY Steelhead Model Summary

The YOY steelhead model forms a crucial portion of the overall riverine steelhead model, but is not explicitly a part of this thesis project. Here I provide a short summary of the YOY steelhead model. For a full description of the YOY steelhead model, I refer readers to Tyler & Rutherford (*in review*).

The YOY steelhead model begins at spawning and ends at the conclusion of the first year when the steelhead have completed the egg, alevin, fry, and parr life stages. Spawning occurs between days 80 and 140 on days with water temperature between 2 and 14 °C. Cells suitable for spawning must have a minimum depth of 0.6 m, maximum water velocity of 0.75 $m \cdot s^{-1}$ and a substrate that is 10-50% gravel. The number of eggs spawned by each female depends upon her weight.

Eggs and alevin are modeled as redd cohorts with development a function of temperature and decreases in number a function of mortality. Sources of mortality included predation, scour, and siltation.

The YOY steelhead model follows fry and parr as individuals because at the fry stage individuals begin to defend territories and make movement and foraging decisions that do not depend entirely on the physical environment. The fry stage begins when individuals complete development through the alevin stage and at a length of 20 mm. Individuals graduate to the parr stage when they reach 40 mm. The model for the fry and parr stages mirrors that described below for the yearling life stages, thus only a brief summary is provided here.

Foraging and growth of fry and parr follow well established models. Foraging is based on the approach of Gerritsen & Strickler (1977) in which fish forage from a volume of water defined as the cylinder of water that passes them in the period of time that they spend actively foraging. The fraction of food items that reside in the volume of water searched depends primarily upon the water velocity with increases in water velocity resulting in a decrease in capture rate. Growth follows the "Wisconsin" bioenergetics model with stage-specific parameters used for the fry and parr life stages (Tyler & Bolduc, *in review* (Appendix A)).

Mortality sources for fry and parr include, in order of importance, predation, temperature extremes, and starvation. Predation follows a length-based function to reflect the fact that larger fish more effectively escape predators. Temperature-based mortality reflects the fact that steelhead do not survive well at temperatures exceeding 23 °C. Starvation mortality occurs when an individual's weight drops to 50% of that expected for a fish of its length.

Fry and parr move about the simulated stream with algorithms that aim to maximize individual fitness, in this case, maximizing growth while minimizing the

probability of mortality. The logic behind the algorithm is that individuals with a low expectation of fitness in their current location will move. Low fitness results from either low foraging and growth rate or high probability of mortality. When moving to a new cell, individuals randomly select to move either upstream or downstream.

Riverine Steelhead Model

The riverine steelhead IBM runs for multiple years and every year a new spawning population is generated. The simulations use the same number of spawning females each year regardless of smolt production since steelhead are a highly stocked species in the Manistee River and natural production represents only a small fraction of the returning spawning population each year (Horne et al., 2004). The characteristics of the spawning population change from year to year and every simulation year in the model is independent of the previous year except for the yearling class. The number of individuals in a yearling age class is dependent upon the survivorship of the class from the previous year.

In the riverine steelhead IBM yearling are modeled as true individuals in the same manner as the fry and parr in the YOY steelhead model. Both the fry and parr stages have been modified slightly from the YOY steelhead IBM. The yearling stage follows the same rules as the YOY individuals for foraging, growth, mortality, and movement functions. The functions that determine foraging and growth are the same for all individuals, but there are differences in the parameters that make each function different for all three stages.

Foraging and Growth

Steelhead that survive through the YOY stages automatically graduate to the yearling stage. To grow, each individual must forage during daylight hours for food to consume. There are different foraging functions for station holders and floaters.

Station holders, individuals that obtain a feeding station, feed on food items that are within their reactive distance and passing by their feeding station. Feeding stations are assigned by a weight-based dominance ranking in each cell, and individuals that do not acquire a feeding station are known as floaters. Floaters encounter fewer prey items and are subject to local density effects that do not affect station holders. After the fish forages for food items it must then consume them.

Consumption is a function of the volume searched by the fish, prey density (equation 1), and the probability of capture (P_{cap}). Consumption cannot exceed the maximum consumption (C_{max}) determined by bioenergetics models (Hanson et al., 1997). Fry, parr, and yearling all use the same prey density function, but it is the probability of capture that allows the yearling to consume more food than individuals from the fry and parr stages. Fry and parr use the same P_{cap} function as the one used in the YOY steelhead IBM, but the yearling use a different P_{cap} function (equation 2).

$$P_{cap} = \frac{0.985 - 0.048V + 0.00056V^2 + 0.0046T}{1 - 0.053V + 0.0013V^2 + 0.0063T} \cdot S_{cap} \qquad (2)$$

Probability of capture is a function of water velocity (V), temperature (T) (Hill & Grossman, 1993), and seasonal probability of capture (S_{cap}). Velocity determines how much food will pass by a fish, since they are drift feeders and depend on food items in the current. Temperature affects the activity level of the fish and as water temperatures

increase so does drift foraging rates (Van Winkle, 1998). Seasons also affect the responsiveness of individuals to food items drifting in the current (Wankowski, 1981).

$$S_{cap} = 0.04 + \left(\frac{0.1055}{1 + \exp(-(day - 244)/10)} \right) \cdot \left(1 - \left(\frac{1}{1 + \exp(-(day - 62)/18)} \right) \right) \quad (3)$$

To capture the seasonal changes in the foraging behavior of steelhead, the function S_{cap} increases in the spring and summer when steelhead forage actively and decreases in the autumn and winter when their foraging is greatly decreased (Figure 4).

Common bioenergetics models, as the ones first developed by Kitchell et al. (1977), are used to determine an individual's growth in the model. The fry, parr, and yearling use the same bioenergetic equations (found in Hanson et al. (1997)), but the yearling use a different set of parameters than the YOY individuals. The fry and parr use parameters that were developed for YOY steelhead (Tyler & Bolduc, *in review* (Appendix A)), while the yearling use parameters that were developed for older steelhead (Railsback & Rose, 1999). To convert weight into length the model uses $L = 46.73 \cdot W^{0.337}$ (Clark & Rose, 1997). If a fish's energetic costs exceed what it consumes, weight may be lost but length will not decrease.

Mortality

The YOY steelhead model features three forms of mortality; predation, starvation, and temperature extremes. Individuals in the riverine steelhead IBM are still subject to the three mortality functions but the predation mortality has been altered. The YOY steelhead IBM only follows parr through one growing season ending on day 275. After day 275 the river environment changes and individuals incur less predation mortality as

predators migrate out of the area (Figure 5a). Parr predation mortality from day 275 to the end of the year follows equation 4.

$$\mu_{PRED} = 0.018 + 5.0 \cdot L^{-1.85} \quad (4)$$

Once the parr survive to the start of a new year their predation mortality changes to the yearling's predation mortality for the fall to spring season (equation 5; Figure 5b).

$$\mu_{PRED,FS} = 0.0051 + 2.0 \cdot L^{-1.85} \quad (5)$$

Like the YOY steelhead IBM, predation is calibrated to produce an average daily mortality rate (Z) similar to the values observed in the Manistee River (data provided by D. Swank, personal communication, University of Michigan, January 19, 2006). For the spring to fall season, mortality decreases and yearling predation is calculated using equation 6 (Figure 5b).

$$\mu_{PRED,SF} = 0.000052 + 2.0 \cdot L^{-2.6} \quad (6)$$

Starvation and temperature mortality did not change from the YOY steelhead IBM and the yearling adopted the same functions. Starvation occurs when an individual's growth trajectory becomes negative and their body weight falls below 50% of the weight expected for an individual of their length. Temperature mortality function is derived from data presented by Hokanson et al. (1977), where above 22 °C smaller fish incur a greater risk of mortality than do larger fish from the high temperature.

Movement

Simulated movement for fry and parr in the riverine steelhead IBM does not change from the method described in the YOY steelhead IBM and the yearling use the same movement rules as the parr. The movement rules are implemented to allow individuals to move to a different cell in an attempt to maximize their fitness by minimizing the

mortality risk to growth rate ratio. However, there are two exceptions to the movement rules: 1) floaters always move if they are able to find an available station and 2) if an individual loses weight over the past five days they will move to another cell.

Smolting

The only simulated event that is unique to the yearling population is smolting. Figure 6 outlines the smolting rules used by the riverine steelhead IBM (D. Swank, personal communication, University of Michigan, June 21, 2005). Individuals can smolt between days 120 and 150 but they are limited by length and an assigned smolting day. Throughout the smolting period, when an individual reaches the minimum smolting length for their age they are assigned a smolting day. Every age class has a different minimum smolting size that increases with age (Figure 6). Smolting days are assigned by the factor of a size dependant value and an exponential random distribution, and individuals cannot smolt before this given day. When individuals smolt they no longer exist in the model and are assumed to have begun their outward migration to open water to join the adult population.

Model Calibration and Baseline Simulation Results

Simulations of the riverine steelhead IBM last ten years. I decided on ten years after running three baseline simulations for 25 years each. The 25 year simulations showed that the behavior of the model stabilized after about year six and there are no consistent and systematic differences in numbers of steelhead that smolt after the sixth year. Differences in the number of smolts produced from the population in the period from years 6 - 25 result from typical variability within the population (Figure 7). Allowing the model simulations to run ten years provides a stable period at the end of the simulation from which I collect output for later analysis.

To calibrate the yearling population I focused on their growth, mortality, and population size. Calibration was accomplished by altering the seasonal probability of capturing food and predation mortality for the yearling population. The model was considered calibrated when the simulated data was within the 95% confidence interval of the field data. Once the model was calibrated, baseline simulations were generated. Baseline simulations are the initial simulations that closely resemble data collected from the Manistee River before any experimental changes are made to the model. I present and analyze data from the last five years of each simulation and assume that it takes the first five years of the simulation for the model to achieve a steady state that is independent of initial conditions.

The calibration of the model was done by comparing lengths, mortality rates, and densities to data collected on the Manistee River and surrounding tributaries for specific dates (D. Swank, personal communication, University of Michigan, January 19, 2006). The mean lengths for the age-1 (Figure 8) and age-2 (Figure 9) yearling fall near the data

collected from the Manistee River, Little Manistee River, Pine Creek, and Bear Creek. The simulated mean ± 1 standard deviation captures either the observed data or part of the 95% confidence interval, with the exception of the one data point collected in the Little Manistee River for age-2 yearling. This data point does lie within 2 standard deviations of the simulated mean length (data not shown). Around day 120 the mean length of both the age-1 (Figure 8) and age-2 (Figure 9) populations decrease due to the larger individuals smolting from the river.

Daily instantaneous mortality rates ($Z \cdot d^{-1}$) for yearling steelhead in the Little Manistee River from summer to fall 1997 were $Z \cdot d^{-1} = 0.00005$ and for fall 1997 to early spring 1998 were $Z \cdot d^{-1} = 0.005$. The mean daily mortality rate for the last five years of the three baseline simulations were $Z \cdot d^{-1} = 0.000047$ for summer to fall and $Z \cdot d^{-1} = 0.008$ for fall to spring.

The densities for the age-1 (Figure 10) and age-2 (Figure 11) yearling stages fit the densities recorded for all of the surrounding tributaries for the same age classes. In the model, steelhead are subject to different seasonal mortality rates. From the spring to fall the steelhead experience less mortality than in the fall to spring season (Figures 10 and 11). A sudden decrease in population densities can be seen around day 120, this is a result of individuals smolting.

Simulation experiments in this model focus on changing water temperature, discharge rates, and spawning female population from their baseline values. The temperature baseline was calculated using the mean temperature collected at Tippy Dam on the Manistee River from 1997-1998 with daily variance generated as described by Tyler & Rutherford (*in review*) (Figure 1). Baseline daily discharge rates for a year were

randomly selected from the field data collected from 1990 to 1998 (Figure 3). Baseline spawning population was set to 3000 females to be consistent with the size of the adult spawner harvest in the Manistee River.

Simulation Experiments

I designed the simulation experiments to reveal how management decisions that change the Manistee River environment and spawning populations may affect the number of individuals that smolt each year. To analyze such changes I used three sets of simulation experiments. Each set was run in triplicate and altered one of three variables from the baseline simulations: number of spawning females, daily discharge, and water temperature (Table 1).

The simulation experiments that focused on the number of spawning females consisted of five different population sizes. Given the baseline simulations, which operated with 3000 spawners every year, I increased and decreased spawning numbers leaving the baseline value in the middle of the range. Spawning numbers used in the simulations were 750, 1500, 6000, and 12000.

The daily discharge set of simulations consisted of two different experiments. The first experiment had two trials using the average low and average high discharge rates from the data set of discharge rates observed at Tippy Dam in the 1990s. Using the 9-year daily discharge data set, I averaged every year to form a list of low to high average discharge rates (Table 2). The low discharge trials randomly chose from the three years of data that had the lowest averages (1991, 1995, and 1998). Likewise, the high discharge trials randomly chose from the three years of data that had the highest discharge average (1992, 1993, and 1994). The second discharge experiment used multipliers on the 9-year daily discharge data sets. Multipliers of 0.5, 0.75, 1.0, 1.25, and 1.5 were applied to the discharge rates to generate discharge rates that were above or below the average discharge.

To analyze water temperature I changed the temperatures during the mid-summer months. During the summer periods, water temperatures were either increased or decreased by 2, 5, or 10 °C, while winter temperatures remained the same as the baseline temperatures (Figure 12). Daily temperatures in all of the experiments still varied randomly as described in the model description.

In this thesis I do not simulate a combination of all the experimental treatments. In a full factorial experiment analyzing the YOY steelhead IBM Tyler & Rutherford (*in review*) found that there were no interactions between spawning number, water temperature, and discharge rate. In the riverine steelhead IBM the yearling stage is fundamentally the same as the fry and parr stages from the YOY steelhead IBM. With the similarities between the life stages I decided against a full factorial experiment as I felt this would not provide any new information about the steelhead population.

Results

Every treatment value (e.g., lowering temperature by 10 °C) consisted of three simulations making a total of 15 data points for each treatment in an experiment (Table 1). The primary response variable I examine here is the number of smolts produced each year. When an individual is identified as a smolt, this does not mean that the individual successfully migrates out of the river. A smolt in the riverine steelhead IBM is an individual that has reached the smolting requirements and will begin its migration out of the river.

Spawning Population

Increasing the number of spawning females resulted in a nearly linear increase in the number of smolts produced for spawning female numbers equal to or below baseline levels. Increasing the number of spawning females above baseline levels showed remarkably little difference in the number of smolts produced (Figure 13a). The treatment with 6000 spawners yielded the highest average of smolts (1757 smolts) followed by the 12000 (1664 smolts) and 3000 (1406 smolts) spawner treatments (Table 3). The number of spawners did not affect the mean weight of the individuals that smolted (Figure 13b). Although the 6000 spawner treatment had the highest average for smolting weight (Table 3) there is no statistical difference between the different treatments (One-Way ANOVA, $P = 0.3830$).

The effect of spawner number on smolts produced led me to examine the population dynamics of the yearling life stage a bit more closely. In particular, I examined the relationship between the number of individuals surviving the YOY life stages as parr and the number of age-1 and age-2 smolts produced in the subsequent

years. Results suggest a linear relationship between the number of parr entering the yearling stage and the number of age-1 smolts ($r^2 = 0.5047$; Figure 14a) and age-2 smolts ($r^2 = 0.3610$; Figure 14b). The linear relationship between these parr number and age-1 and age-2 smolts is suggested by examining the upper bound of the plots in Figure 14. Obviously, parr number is not the only determinant of age-1 and age-2 smolts as demonstrated by the low r^2 values and the range of values below that upper bound. However, there appears to be a strong upper bound to the number of smolts that can be produced and that bound seems to be met at spawning population numbers of about 6000 spawning females.

Discharge Rates

Average Discharge

The average discharge experiments randomly selected the discharge data for a specific year of the ten-year simulation from either the three years with the highest or the three years with the lowest daily discharge average depending on the high or low treatment. The simulations that used the actual data for the daily discharge showed no effect of discharge treatment on the number or weight of smolts produced each year (Figure 15).

The Manistee River is one of the most constant flowing rivers in the United States and therefore the average high and low treatments lack any extreme discharges such as those created from droughts and floods (M. Wiley, personal communication, University of Michigan, May 31, 2006). A simple computation of the mean daily discharge under the low, baseline, and high discharge treatments used in this simulation experiment demonstrate a relatively small difference in the treatments (Table 2).

Discharge Multiplier

To produce a change in the model river's flow that was not seen in the average high or low experiments I employed discharge multipliers of 0.5, 0.75, 1.0 (baseline), 1.25, and 1.5 to the baseline discharge. Changes in discharge using the discharge multiplier approach showed a notable effect of discharge on the number of smolts each year (Figure 16a), although the overall weight of smolts seemed insensitive to changes in the discharge multiplier (Figure 16b). More smolts are produced when the discharge multiplier is 1.0 and 1.25 in comparison to the 0.5 and 0.75 multipliers (Figure 16a). The multiplier of 1.5 has a larger number of smolts than the 0.5 and 0.75 multipliers but less than the 1.0 and 1.25 multipliers (Figure 16a). Overall, these simulations suggest that baseline discharge levels are best for smolt production and that lower discharge levels are a greater problem for smolt production than are higher discharge levels.

The age distribution of smolt number (Figure 17a) and mean weight of age-1 and age-2 smolts (Figure 17b) showed discernable differences based on discharge multiplier. The smolt age distribution changes from a predominantly age-2 smolt to an age-1 smolt as the discharge multiplier increases (Figure 17a). The mean smolt weight of the age-1 population increases slightly with the discharge multiplier ($r^2 = 0.2118$) but not as much as the increase seen with the weight of the age-2 population and discharge multiplier ($r^2 = 0.6238$; Figure 17b).

An increased number of parr entering the yearling stage correlated with a larger number of age-1 smolts for the highest discharge treatment (1.5; $r^2 = 0.8515$), while for age-2 smolts the lowest discharge treatment (0.5) shows an increased number of smolts as the number of entering parr increases ($r^2 = 0.9453$; Figure 18). There is a slightly higher number of parr graduating to the yearling stage with the baseline and lower discharge

multipliers than with the higher discharge multipliers which is consistent with the results reported by Tyler & Rutherford (*in review*) (Figure 18). The increasing number of age-2 smolts is due to the lack of smolting occurring in the age-1 population at the lowest discharge. This is further supported by the lower mean age-1 smolt weight (Figure 17b) revealing the difficulty for individual's to grow to the smolting minimum at the lower discharge rates.

Temperature

The number of smolts produced with each temperature treatment increased as temperatures decreased. The 5 and 10 °C above baseline trials did not produce any parr that survived to graduate into the yearling stages, while the 2 °C above baseline trial saw the fewest smolts produced (Figure 19a). The 10 °C below baseline trial produced the overall largest number of smolts (Figure 19a). The breakdown of the age-1 and age-2 smolt numbers revealed that the age-1 population is the dominant smolting class driving the decrease seen in Figure 19a. The age-2 smolt numbers remains relatively constant across all temperatures with a slight decrease in the 2 °C above baseline treatment. The mean smolt weights for the smolting population remained relatively constant over the temperature gradient (Figure 19b) and with the colder temperature trials more parr entered the yearling stage (Figure 20). For the age-1 population, as more parr graduated to yearling the number of smolts increased ($r^2 = 0.6192$) but this correlation was not as strong for the age-2 population ($r^2 = 0.3648$).

Discussion

The simulation experiments revealed a density dependent signal in the number of individuals that smolt as the number of spawning females increased. Tyler & Rutherford (*in review*) reported density dependence in the fry stage and it appears this density dependence may be producing the limitations seen in smolting numbers. The number of yearling smolting generally increased as the number of parr entering the stage increased (Figure 14), but the number of parr entering is no greater for the 12000 spawners than the 6000 spawners, thus revealing density dependence prior to the yearling stage. Density dependence in an earlier life stage could also explain why there is no evidence of weight loss as the higher spawning populations are introduced (Figure 13). Typically, if the population is affected by density dependence there is more competition for food resulting in slower growth rates (Cowan et al., 2000). This would result in lower average weights for the individuals in the treatments where density dependence is present and no such change in smolt weight was seen in these simulation experiments.

The water discharge rates from Tippy Dam during the 1990s vary little as evidenced by the simulations of "high" and "low" discharge simulations using the actual data from that period. Simulations of the riverine steelhead IBM suggest that the differences in discharge during the 1990s had little effect on either the size of the steelhead population or average weight of the smolts (Figure 15).

Little variation in water discharge exists in the data from the 1990s, thus I conducted the second simulation experiment, in which discharge was altered by using a multiplier on the baseline discharge, to determine the potential consequences of significant changes in the amount of water running down the Manistee River. If the

discharge rates were altered from the current regime, the riverine steelhead IBM shows that a decrease may adversely affect the number of individuals smolting from the river every year (Figure 16a). Larger, older smolts have a better chance of surviving their migration downstream than smaller, younger smolts because they are less prone to predation (Marschall et al., 1998; Woldt & Rutherford, 2004). Even though the smolting populations for the simulations with decreased discharge in the second water discharge experiment are predominantly age-2, these individuals have the lowest average weights out of all the experiment's treatments. The decrease in weight can be explained by the feeding mechanism employed by the model. All steelhead are modeled to be drift feeders and slower currents would provide less food to the fish, therefore inhibiting the growth rate of the population. While this is a prominent factor in the model, it may not have as severe of an effect in the real world since fish will actively search out other food sources in the absence of sufficient drift food (Angradi & Griffith, 1990). However, a decrease in weight may still be a reasonable expectation as flow decreases.

When discharge rates were increased in the second discharge experiment interesting results occurred. The baseline and close to baseline multipliers produced the overall largest number of smolts (Figure 16a). The baseline discharge rates produced the highest number of age-2 smolts, but did not produce the highest average weights (Figure 17). The weights are slightly higher for the population at the highest discharge multiplier (1.5), but the smolt numbers for this discharge rate are lower than baseline. Without knowing the survival rates for the migration downstream it would be difficult to determine which discharge rate would actually produce more successful smolts. One would have to analyze the ratio of individuals ready to smolt and individuals that

successfully smolt. The riverine steelhead IBM identifies the baseline and slightly above baseline discharge rates as having the greatest potential for increasing steelhead recruitment.

The riverine steelhead IBM predicts that as the mid-summer water temperatures decrease the steelhead population produces more smolts. Previous studies have found survivorship for the YOY life stages to increase with cooler water temperatures (Woldt & Rutherford, 2004; Tyler & Rutherford, *in review*) and the riverine steelhead IBM agrees because there are more parr entering the yearling stage as temperatures decrease. Generally, as there are more parr the number of age-1 smolts increases (Figure 20a), however, this is not seen in the age-2 population. The number of age-2 smolts does not increase with water temperature even though there are more parr entering the yearling stage (Figure 20b). The relatively constant age-2 smolt number at the different temperature regimes is likely a result of the amount of age-1 individuals smolting. Increases in the number of parr produced correlates with an increase in the number of age-1 smolts in a relatively tight relationship ($r^2 = 0.6192$). The relationship between parr number and age-2 smolts is not as tight ($r^2 = 0.3648$) as evidenced by the much greater variability seen in their numbers (Figure 20).

The most prominent result of the temperature treatments was the inability for steelhead to survive at the 5 and 10 °C mid-summer temperature increases. Even at the 2 °C above baseline temperature treatments the population suffered, producing the fewest smolts of all the treatments. The effect of increased temperature on smolt production appears to occur during the YOY stages since no parr survived to the older stages when temperature was increased by 5 and 10 °C and the lowest number of parr survived in the

treatments with a 2 °C temperature increase (Figure 20). The weight of the smolts is reasonably stable across all temperature treatments, indicating that at the higher temperatures the weights of the smolting individuals are not being affected by increased bioenergetic costs. The loss of entire year classes in the YOY portion of the model results primarily from the temperature-based mortality of YOY steelhead derived from results of experiments by Hokanson et al. (1977). However, temperature extremes that occur unexpectedly in a previous laboratory study (Tyler & Bolduc, *in review* (Appendix A)) did show that temperatures of 23 °C could be lethal to yearling steelhead.

The response the steelhead had to increased temperatures in the riverine steelhead IBM can help show the impact that a rise in water temperature can have on the steelhead population. Ambient air temperatures can increase water temperature (Eaton & Scheller, 1996) and as the model shows, even a 2 °C increase has adverse affects on steelhead populations. Horne et al. (2004) showed that temperatures could be lowered by changing the dam from top to bottom withdrawal, but even this could not decrease water temperatures by 5 or 10 °C. Boer (2000) predicts global mean temperatures will rise by 1.7 °C by 2050 and 2.7 °C by 2100 while Eaton and Scheller (1996) forecast a 5.10 °C increase in air temperature over the Manistee River area after the atmospheric CO_2 concentration doubles. With the expectations of such temperature increases, bottom withdrawal may be sufficient for a short-term solution, but may not be sufficient for long-term water temperature control. However, the relationship between increased air temperature and water temperature in tributaries of Lake Michigan, like the Manistee River, is unclear. Such rivers receive significant amounts of their water via groundwater sources which are much cooler than surface waters. Global warming may increase

ambient air temperature, but will also alter the input of water to rivers and may alter the balance of surface versus ground water inputs in a way that mitigates the effects on tributary water temperatures (M. Wiley, personal communication, University of Michigan, March 22, 2006).

The riverine steelhead IBM produces results that may be able to help management increase steelhead recruitment. Specifically the discharge simulations emphasize the need to maintain the current, or possibly introduce higher, discharge rates to maintain and possibly increase steelhead recruitment. The model also shows that colder water temperatures only favor steelhead recruitment. Finally, the riverine model highlights the importance of the YOY populations. To maximize the number of smolts every year the fry stage needs to be more thoroughly analyzed to maximize this population. The fry stage has been a factor of density dependence in previous studies (Elliott, 1989, 1993; Tyler & Rutherford, *in review*) and appears to be the limiting factor in increasing smolt numbers when increasing spawning populations in this study.

References

Angradi, T. R. and Griffith, J. S. 1990. Diel feeding chronology and diet selection of rainbow trout (*Oncorhynchus mykiss*) in the Henry's Fork of the Snake River, Idaho. Canadian Journal of Fisheries and Aquatic Sciences 47: 199-209.

Babbitt, B. 2002. What goes up may come down. BioScience 52: 656-658.

Boer, G. J., Flato, G., and Ramsden, D. 2000. A transient climate change simulation with greenhouse gas and aerosol forcing: projected climate to the twenty-first century. Climate Dynamics 16: 427-450.

Brock, T. D. 1981. Calculating solar radiation for ecological studies. Ecological Modelling 8: 109-132.

Clark, M. E. and Rose, K. A. 1997. Factors affecting competitive dominance of rainbow trout over brook trout in southern Appalachian streams: Implications of an individual-based model. Transactions of the American Fisheries Society 126: 1-20.

Cowan, Jr., J. H., Rose, K. A., and DeVries, D. R. 2000. Is density-dependent growth in young-of-the-year fishes a question of critical weight? Reviews in Fish Biology and Fisheries 10: 61-89.

Covington, J. S. and Hubert, W. A. 2003. Trout population responses to restoration of stream flows. Environmental Management 31: 135-146.

DeAngelis, D. L., Barnthouse, L. W., Van Winkle, W., and Otto, R. G. 1990. A critical appraisal of population approaches in assessing fish community health. Journal of Great Lakes Research 16: 576-590.

Doyle, M. W., Harbor, J. M., and Stanley, E. H. 2003. Toward policies and decision-making for dam removal. Environmental Management 31: 453-465.

Eaton, J. G. and Scheller, R. M. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41: 1109-1115.

Elliott, J. M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. Journal of Animal Ecology 58: 987-1001.

Elliott, J. M. 1993. The self-thinning rule applied to juvenile sea trout, *Salmo trutta*. Journal of Animal Ecology 62: 371-379.

Gerritsen, J. and Strickler, J. R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. Journal of the Fisheries Research Board of Canada 34: 73-82.

Giske, J., Huse, G., and Fiksen, Ø. 1998. Modelling spatial dynamics of fish. Reviews in Fish Biology and Fisheries 8: 57-91.

Grant, J. W. A. and Noakes, D. L. G. 1987. A simple model of optimal territory size for drift feeding fish. Canadian Journal of Zoology 65: 270-276.

Hanson, P. C., Johnson, T. B., Schindler, D. E., and Kitchell, J. F. 1997. Fish bioenergetics 3.0. University of Wisconsin System Sea Grant Institute. Madison.

Hart, D. D., Johnson, T. E., Bushaw-Newton, K. L., Horwitz, R. J., Bednarek, A. T., Charles, D. F., Kreeger, D. A., and Velinsky, D. J. 2002. Dam removal: Challenges and opportunities for ecological research and river restoration. BioScience 52: 669-681.

Hokanson, K. E. F., Kleiner, C. F., and Thorslund, T. W. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile Rainbow Trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34: 639-948.

Horne, B. D., Rutherford, E. S., and Wehrly, K. H. 2004. Simulating effects of hydro-dam alteration on the thermal temperature regime and wild steelhead recruitment in the Manistee River, Michigan. River Research and Applications 20: 185-203.

Huston, M. A., DeAngeliz, D. L., and Post, W. 1988. New computer models unify ecological theory. BioScience 38: 682-690.

Ichthyological Associates. 1990. Instream flow incremental methodology – Hydraulic modeling report for the Tippy project, FERC Project # 2580, Manistee River, Michigan. Report to Lawler, Matuskey and Skelley Engineers, contracted by Consumers Power Company. Lansing, MI.

Jakubiak, J. 1999. River revival. Michigan Sea Grant Upwellings 21:1.

Kitchell, J. F., Stewart, D. J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (*Perca Flavescens*) and walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 34: 1922-1935.

Lytle, D. A. and Poff, N. L. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19: 94-100.

Marschall, E. A., Quinn, T. P., Roff, D. A., Hutchings, J. A., Metcalfe, N. B., Bakke, T. A., Saunders, R. L., and Poff, N. L. 1998. A framework for understanding

Atlantic salmon (*Salmo salar*) life history. Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1): 48-58.

Myrick, C. A. and Cech, Jr., J. J. 2004. Temperature effects on juvenile anadromous salmonids in California's central valley: what don't we know? Reviews in Fish Biology and Fisheries 14: 113-123.

Newcomb, T. J. and Coon, T. G. 1997. Evaluation of alternate methods for estimating numbers of outmigrating steelhead smolts. Michigan Department of Natural Resources, Fisheries Division Report 2045. Ann Arbor, MI.

Ormerod, S. J. 2003. Current issues with fish and fisheries: editor's overview and introduction. Journal of Applied Ecology 40: 204-213.

Osmundson, D. B., Ryel, R. J., Lamarra, V. L., and Pitlick, J. 2002. Flow-sediment-biota relations: Implications for river regulation effects on native fish abundance. Ecological Applications 12: 1719-1739.

Poff, N. L. and Hart, D. D. 2002. How dams vary and why it matter for the emerging science of dam removal. BioScience 52: 659-668.

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., Sparks, R. E., and Stromberg, J. C. 1997. The natural flow regime. BioScience 47: 769-784.

Railsback, S. F. and Rose, K. A. 1999. Bioenergetics modeling of stream trout growth: Temperature and food consumption effects. Transactions of the American Fisheries Society 128: 241-256.

Rand, P. S., Stewart, D. J., Seelbach, P. W., and Wedge, L. R. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Transactions of the American Fisheries Society 122: 977-1001.

Swartzmann, G. L. 1987. Ecological simulation primer. MacMillan. New York.

Thompson, B. E. 2004. Modeling of juvenile steelhead growth and movement in the Pine River, Michigan. Ph.D. dissertation, Michigan State University. East Lansing, MI.

Tyler, J. A. and Bolduc, M. B. *in review*. Individual variation in bioenergetic rates of YOY rainbow trout. Transactions of the American Fisheries Society. (Appendix A)

Tyler, J. A. and Rose, K. A. 1994. Individual variability and spatial heterogeneity in fish population models. Reviews in fish biology and fisheries 4: 91-123.

Tyler, J. A. and Rutherford, E. S. *in review*. River restoration effects on steelhead populations in the Manistee River, Michigan: analysis using an individual-base model. Transactions of the American Fisheries Society.

Van Winkel, W., Jager, H. I., Railsback, S. F., Holcomb, B. D., Studley, T. K., and Baldrige, J. E. 1998. Individual-based model of sympatric populations of brown and rainbow trout for instream flow assessment: model description and calibration. Ecological Modelling 110: 175-207.

Wankowski, J. W. J. 1981. Behavioural aspects of predation by juvenile Atlantic Salmon (*Salmo Salar* L.) on particulate, drifting prey. Animal Behaviour 29: 557-571.

Woldt, A. and Rutherford, E. S. 2002. Production of juvenile steelhead in two central Lake Michigan tributaries. Michigan Department of Natural Resources, Fisheries Division Report 2060. Ann Arbor, MI.

Workman, R. D. 2002. Spawning migrations and habitat selection by steelhead and longnose suckers in the Pere Marquette and St. Joseph Rivers, Michigan. Ph.D. dissertation, Michigan State University. East Lansing, MI.

Table 1. Simulation treatments. Gray boxes indicate baseline values for the treatment.

Treatment	**Value**						
Spawning	750	1500	3000	6000	12000		
Discharge Average	low	baseline	high				
Discharge Multiplier	0.5	0.75	1.0	1.25	1.5		
Temperature (from baseline)	-10 °C	-5 °C	-2 °C	0 °C	+2 °C	+5 °C	+10 °C

Table 2. Average discharge for every year of the 9-year daily discharge data set.

Year	Average Discharge ($m^3 \cdot s^{-1}$)
1990	31.06
1991	30.26
1992	33.63
1993	35.01
1994	31.54
1995	29.49
1996	31.46
1997	30.92
1998	28.21

Table 3. Mean and standard deviation (SD) for number of smolts and smolt weight for each spawning treatment.

	Spawning Number									
	750		1500		3000		6000		12000	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Number of smolts	630	285	972	376	1406	510	1757	462	1664	518
smolt weight (g)	55	12.4	50.5	9.8	56.6	9.9	56.1	20.6	47.7	17.1

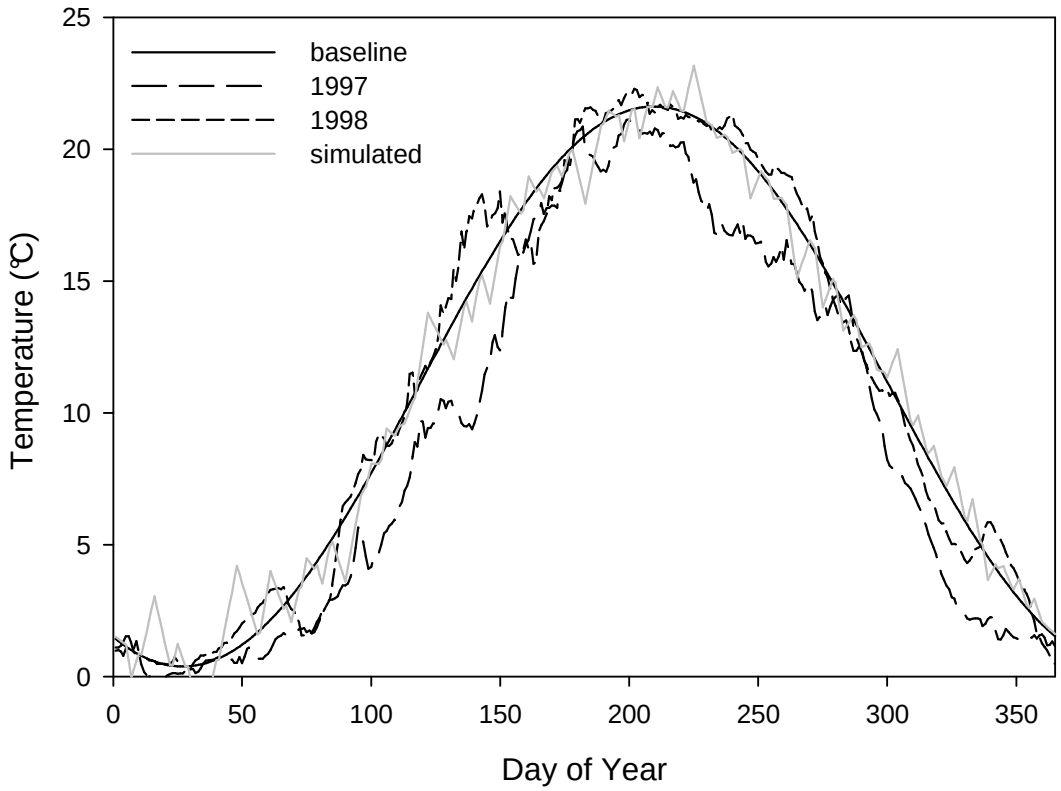

Figure 1. Actual and simulated water temperatures for the Manistee River from 1997 to 1998. Simulated long-term mean temperature used in the model and the variable temperature from one baseline simulation are also shown.

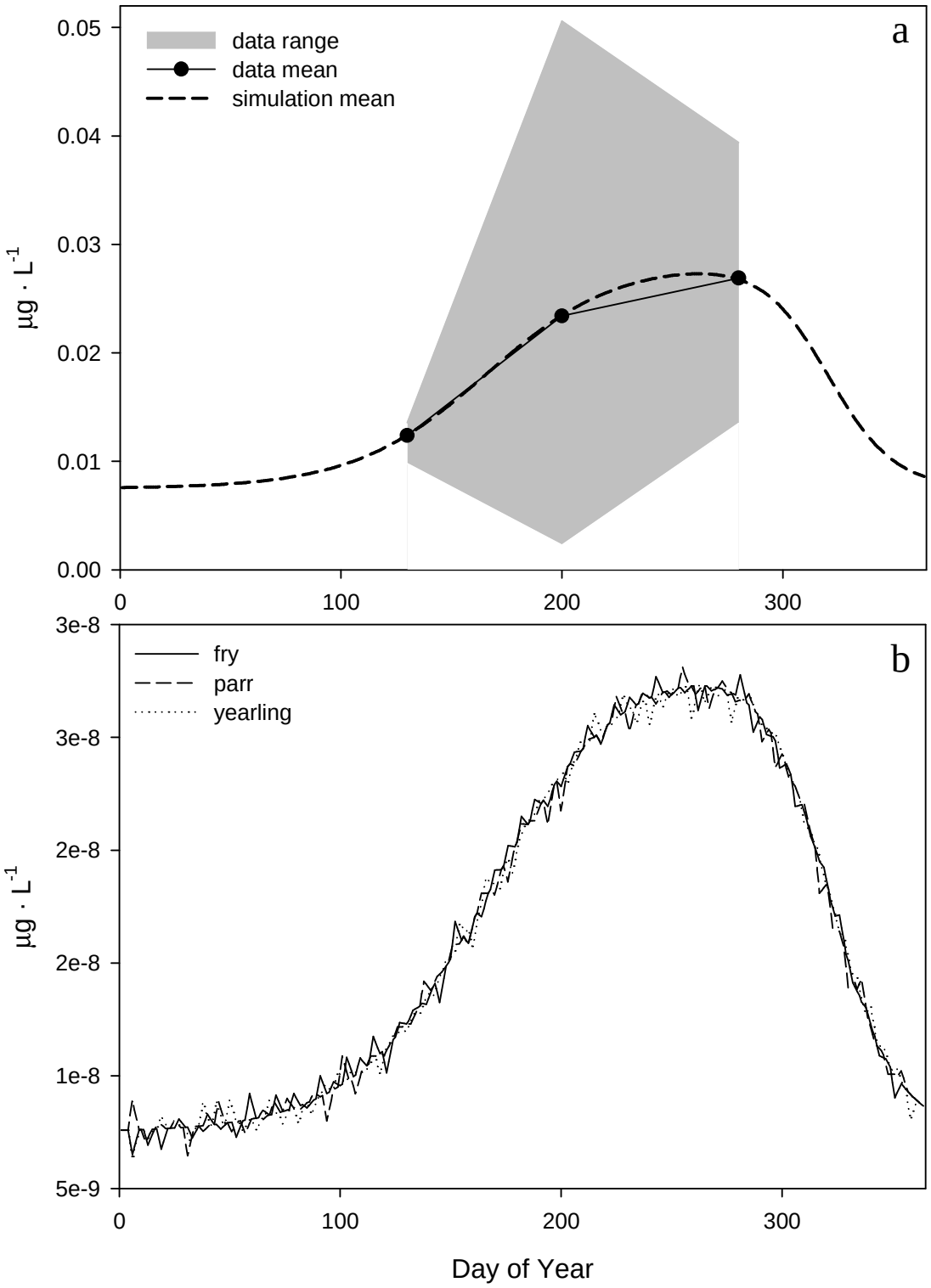

Figure 2. Daily prey densities available for fry, parr, and yearling with mean and the range (maximum-minimum) determined with data from the Muskegon River shown with the mean simulated prey density in the model (a). Fry, parr, and yearling prey densities in each simulation have some random variation from the long-term mean as shown for one simulation year (b).

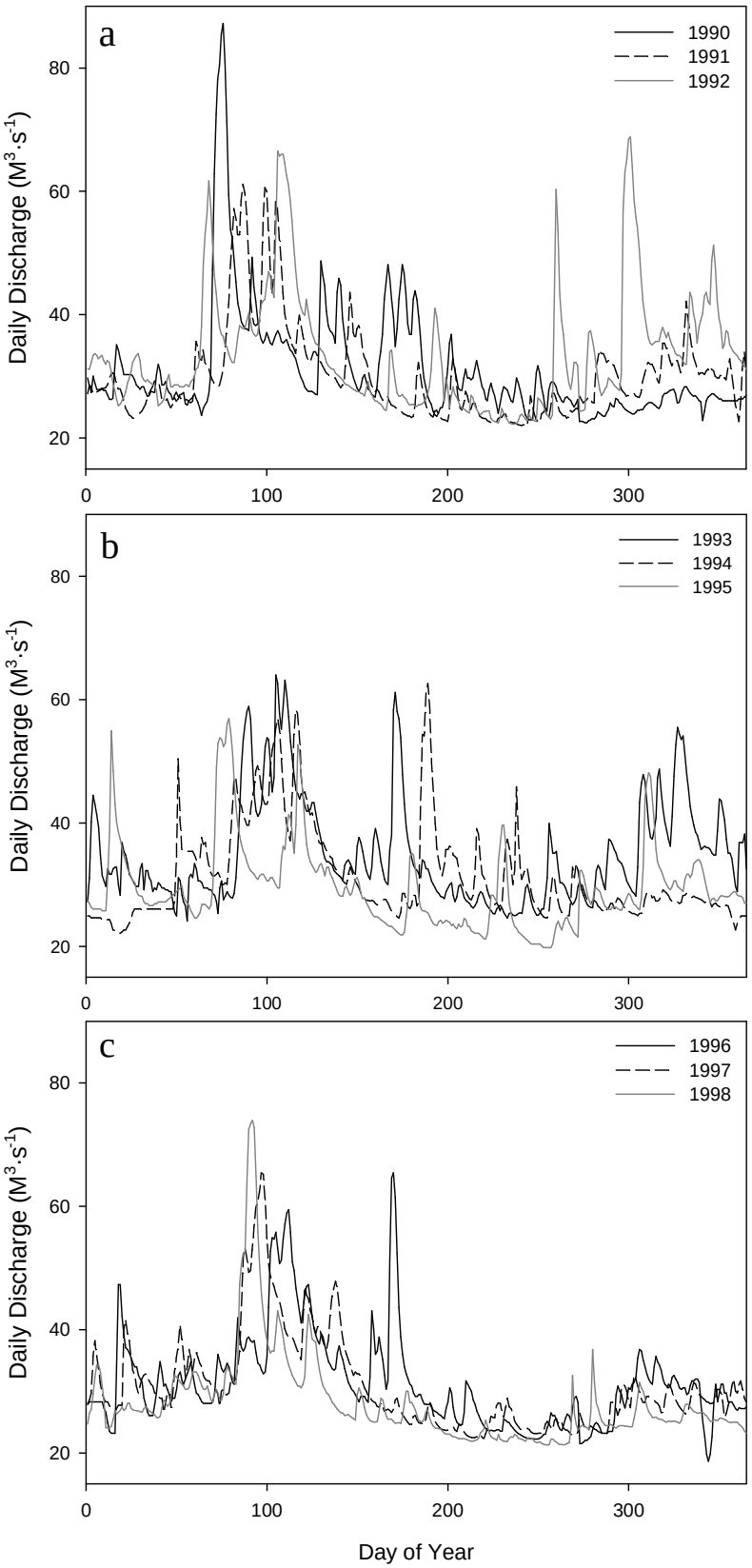

Figure 3. Daily water discharge ($m^3 \cdot s^{-1}$) from Tippy Dam from 1990-1998.

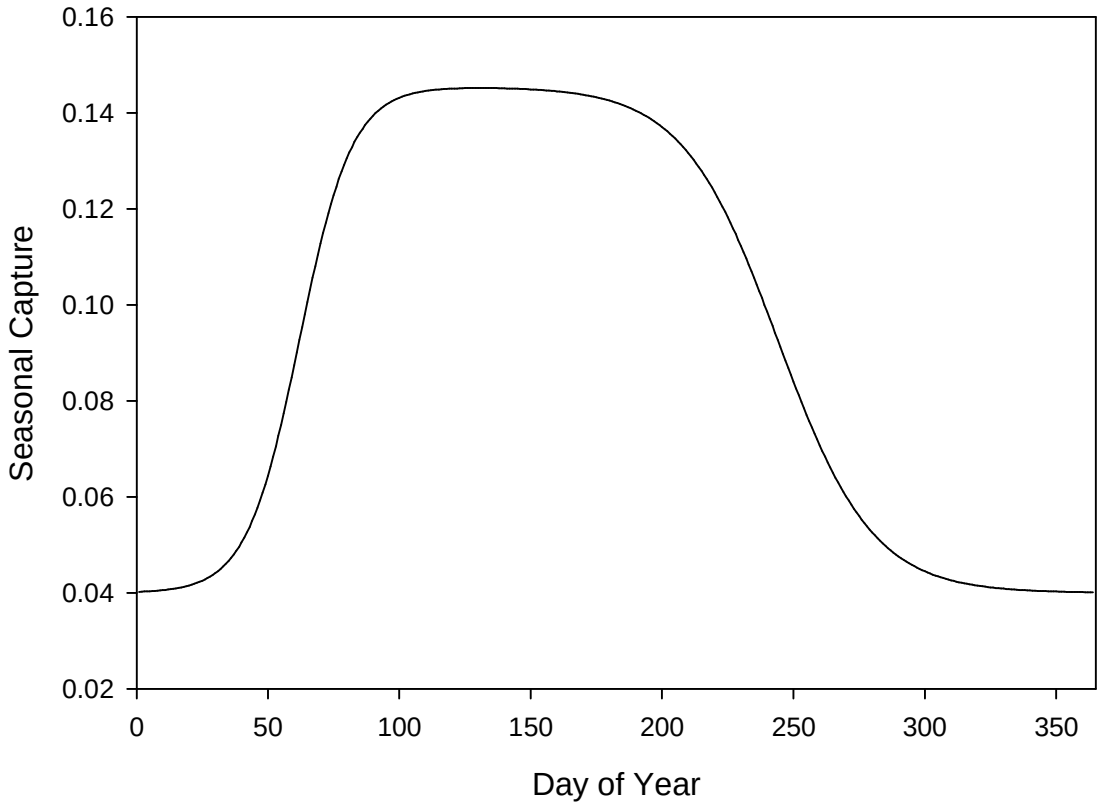

Figure 4. Seasonal probability of prey capture for yearling.

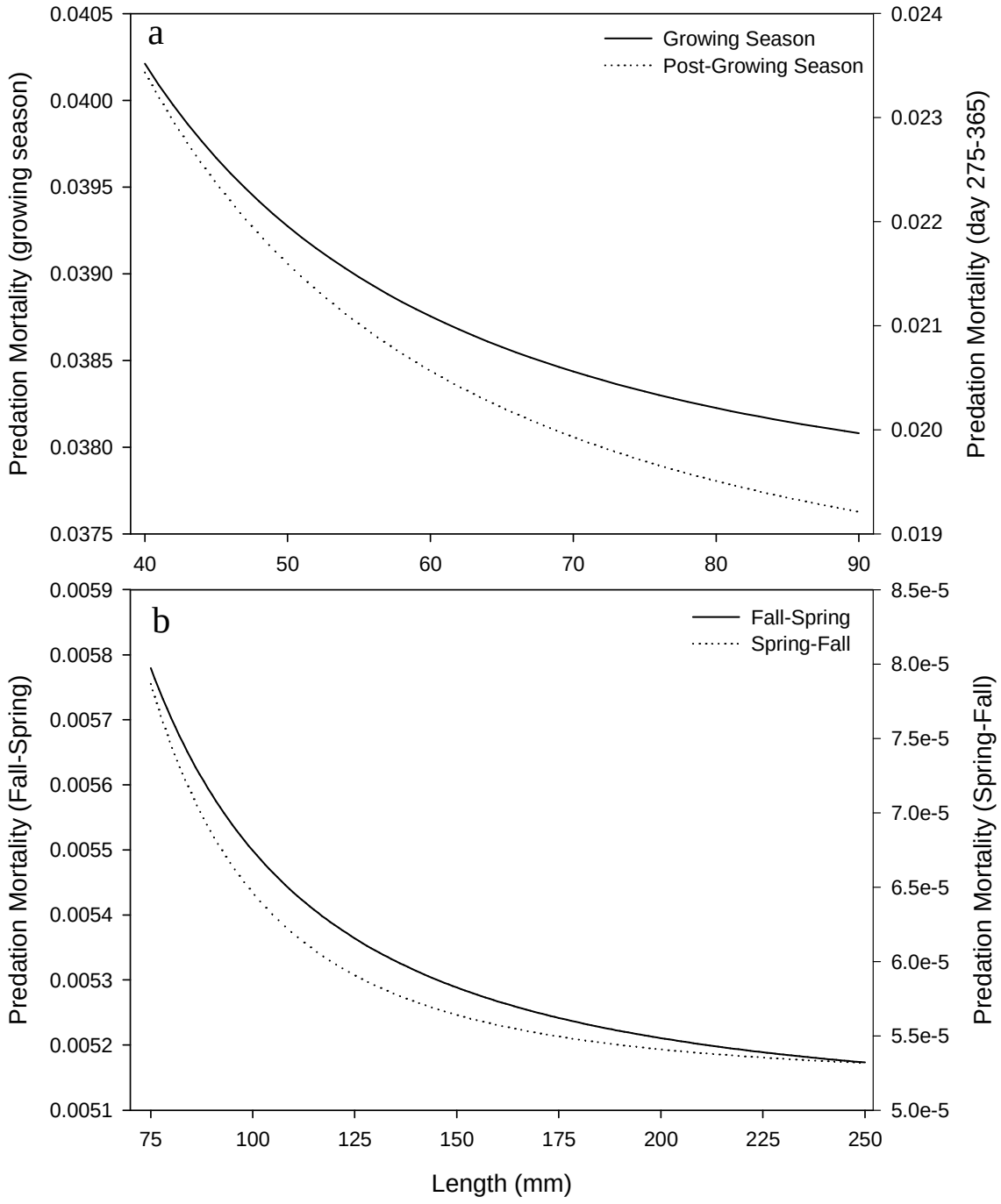

Figure 5. Predation mortality for parr (a) and yearling (b). Parr predation mortality changes at the end of the growing season (day 275) to the end of the year. Yearling predation mortality changes in the spring and in the fall.

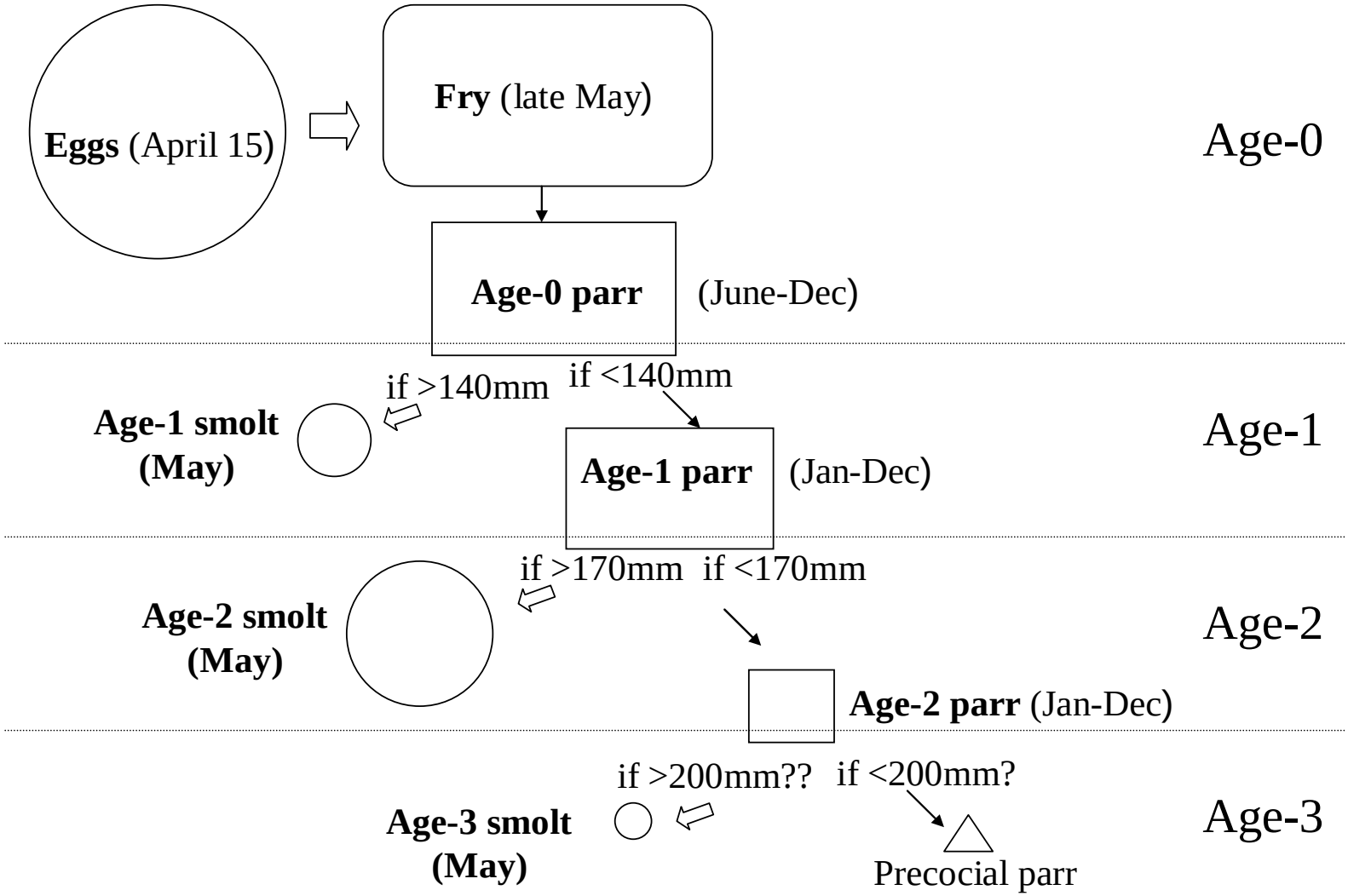

Figure 6. Life-cycle of the steelhead highlighting the smolting rules employed by the riverine IBM. Steelhead start their life as eggs, developing into fry and then parr within the first year of life. At the start of the next year, individuals are now classified as age-1 and they are given the option to smolt if their length is at least 140mm in May. If an individual does not meet the minimum length and survives to the next year, their age increases and they are now considered age-2 individuals. In May, if age-2 individuals are a minimum of 170mm they will smolt, if not they become age-3 and have the opportunity to smolt the following May if they are 200mm. If an age-3 individual does not smolt they are given the same opportunity to smolt as age-3 individuals every year. (Outline provided by D. Swank)

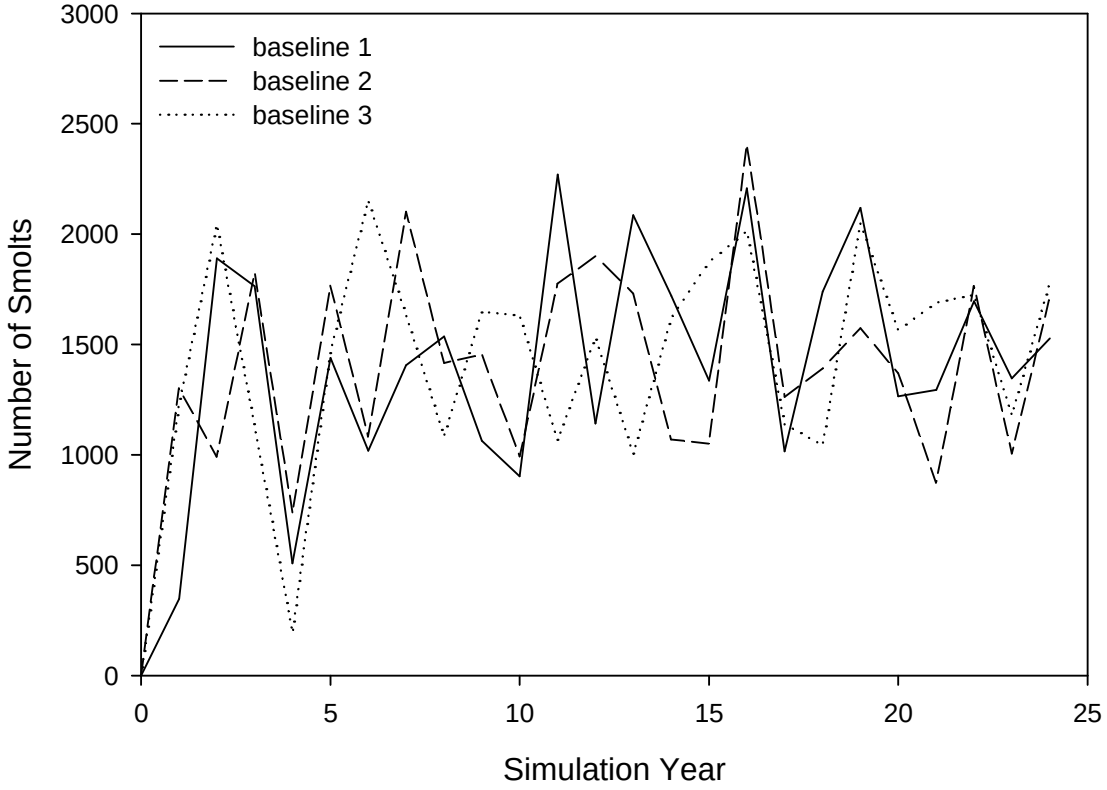

Figure 7. Smolt numbers for baseline simulation experiments that ran for 25 years.

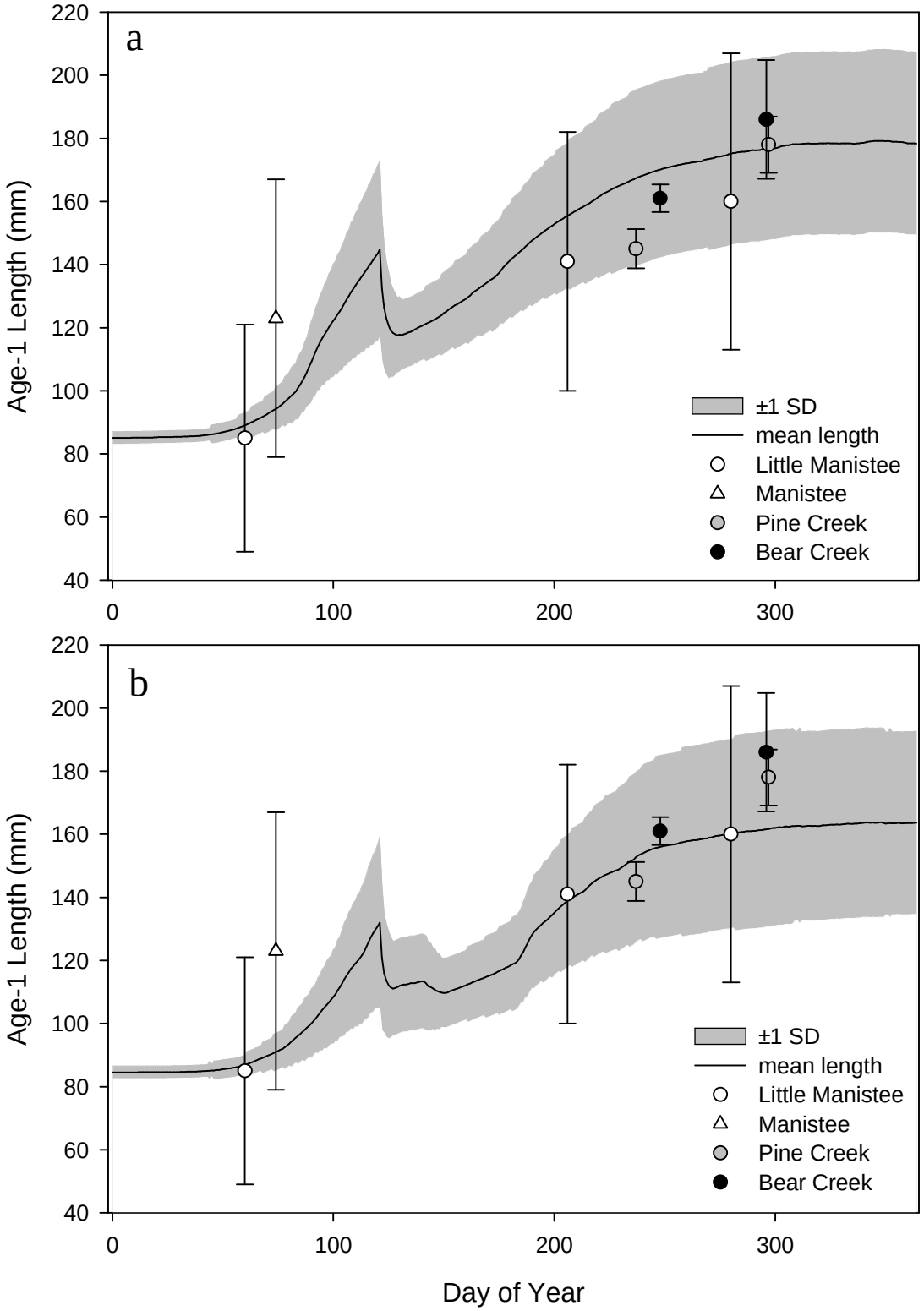

Figure 8. Mean length of simulated age-1 yearling ±1 standard deviation (SD) for year 8 (a) and year 9 (b) from one randomly selected baseline simulation. Data points show length data collected for age-1 steelhead from the Manistee River and surrounding tributaries and their 95% confidence interval.

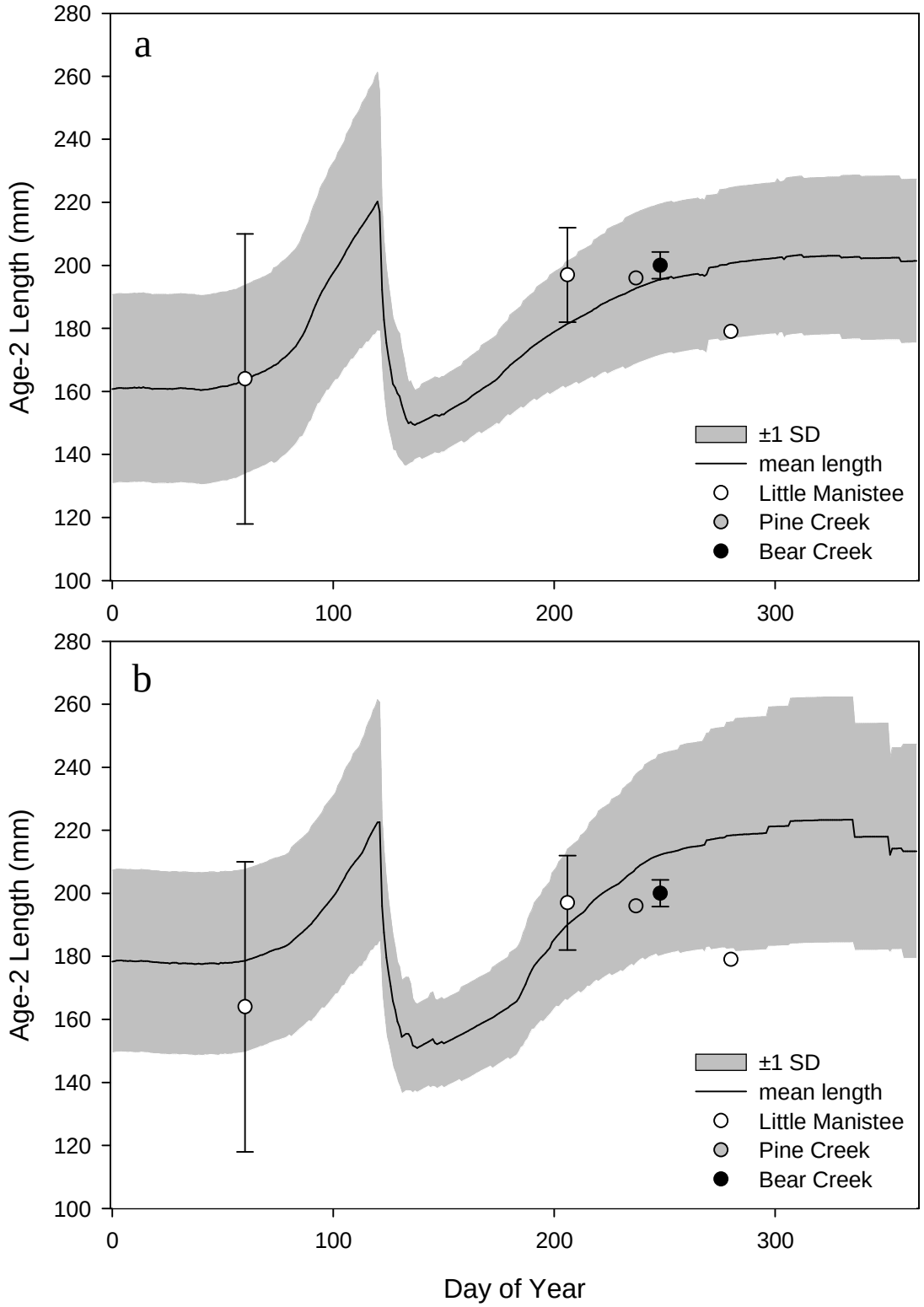

Figure 9. Mean length of simulated age-2 yearling ±1 standard deviation (SD) for year 8 (a) and year 9 (b) from one randomly selected baseline simulation. Data points show length data collected for age-2 steelhead from the surrounding tributaries of the Manistee River and their 95% confidence interval.

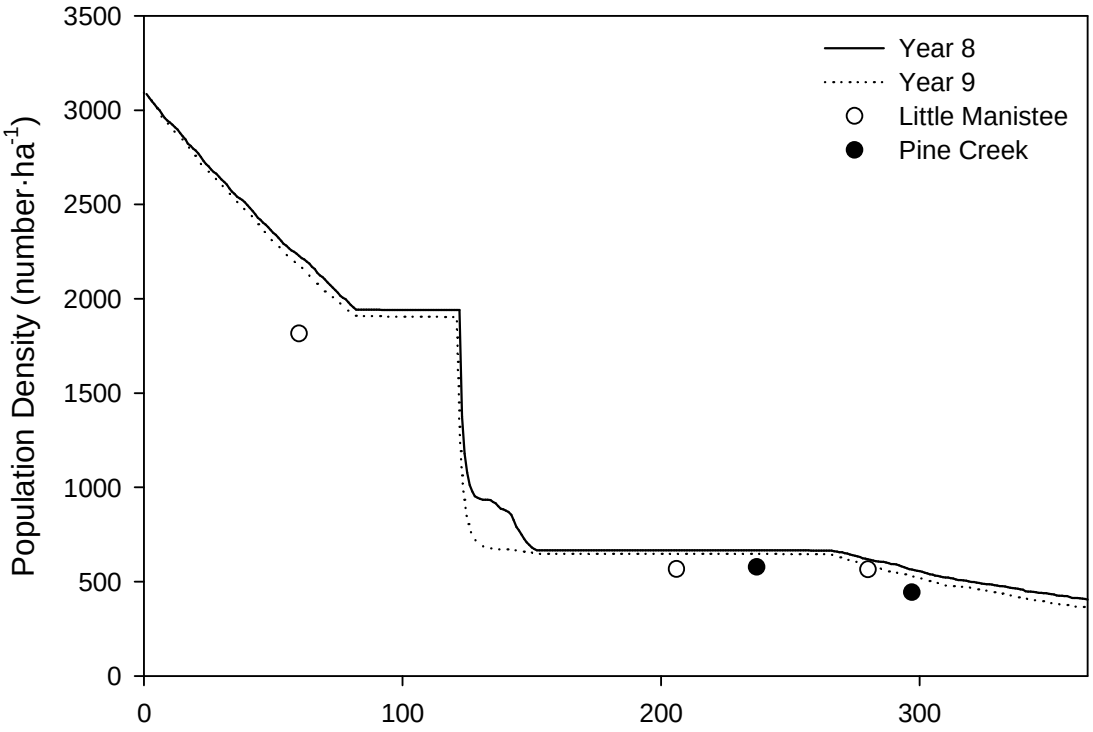

Figure 10. Density of age-1 yearling from years 8 and 9 of a baseline simulation. Also included are field data for age-1 steelhead in surrounding tributaries of the Manistee River.

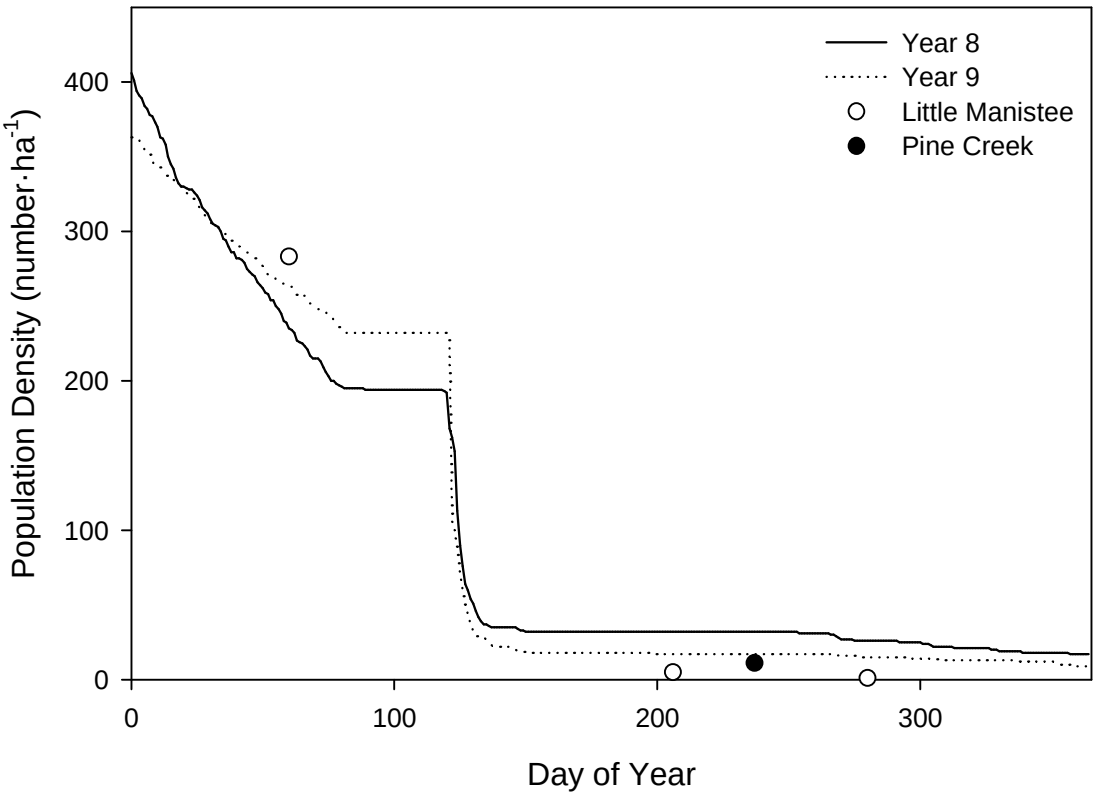

Figure 11. Density of age-2 yearling from years 8 and 9 of a baseline simulation. Also included are field data collected for age-2 steelhead in surrounding tributaries of the Manistee River.

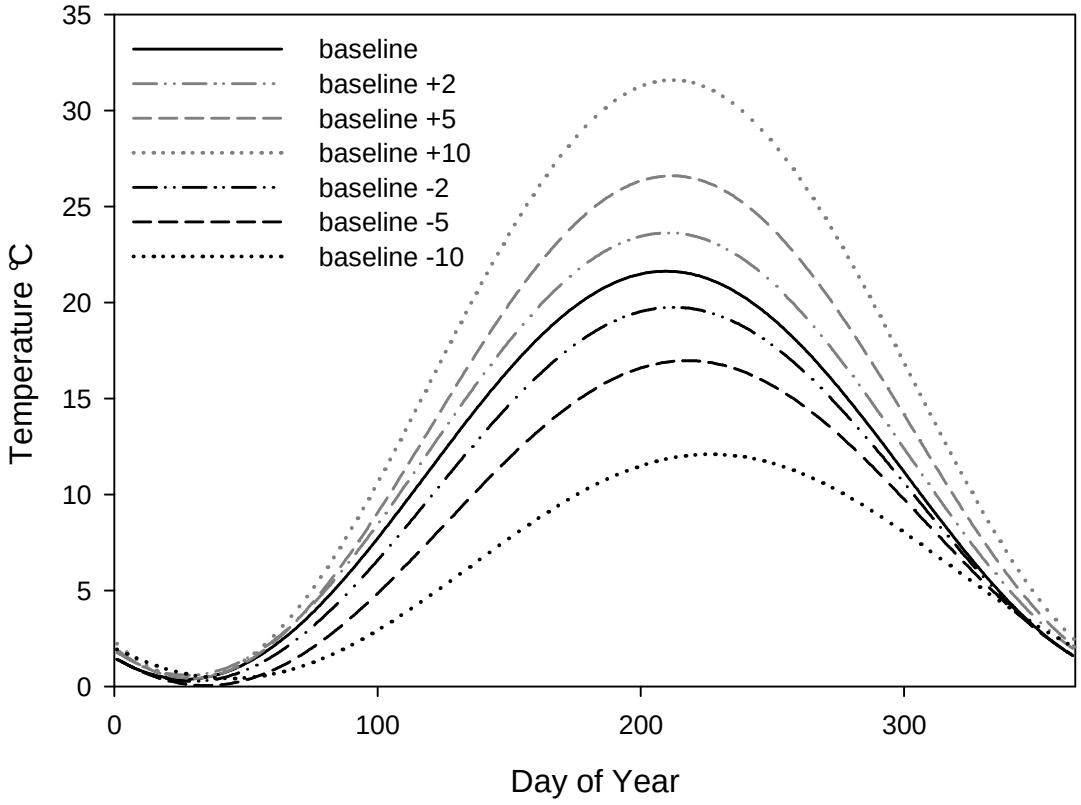

Figure 12. Mean daily water temperatures for simulation experiments. The mid-summer temperature was reduced by 2, 5, and 10 °C and increased by 2, 5, and 10 °C. Each simulation will have random variation from the mean temperature for the treatment shown here.

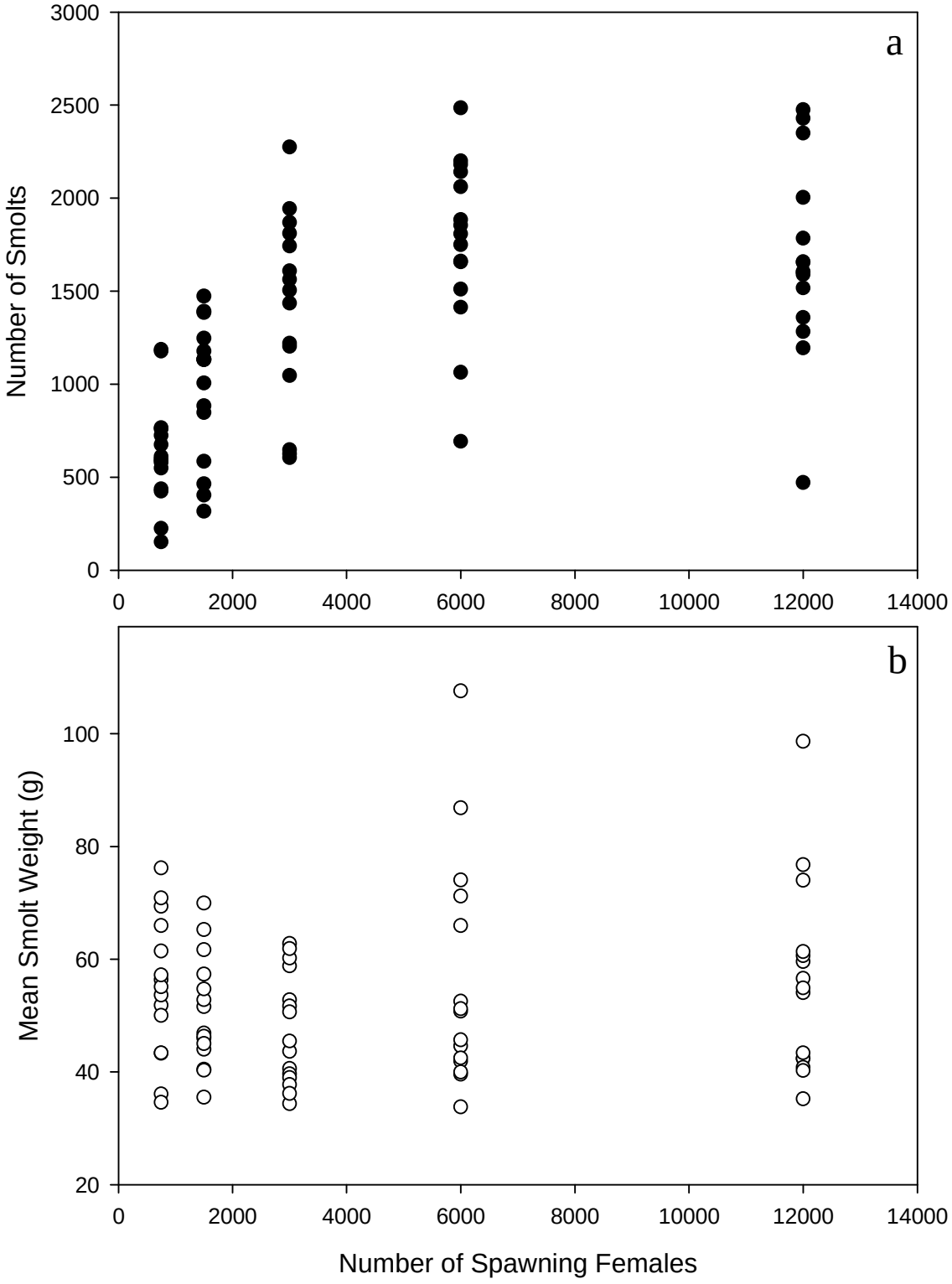

Figure 13. Changes in number of total smolts (a) and mean weights (b) as number of spawning females is altered.

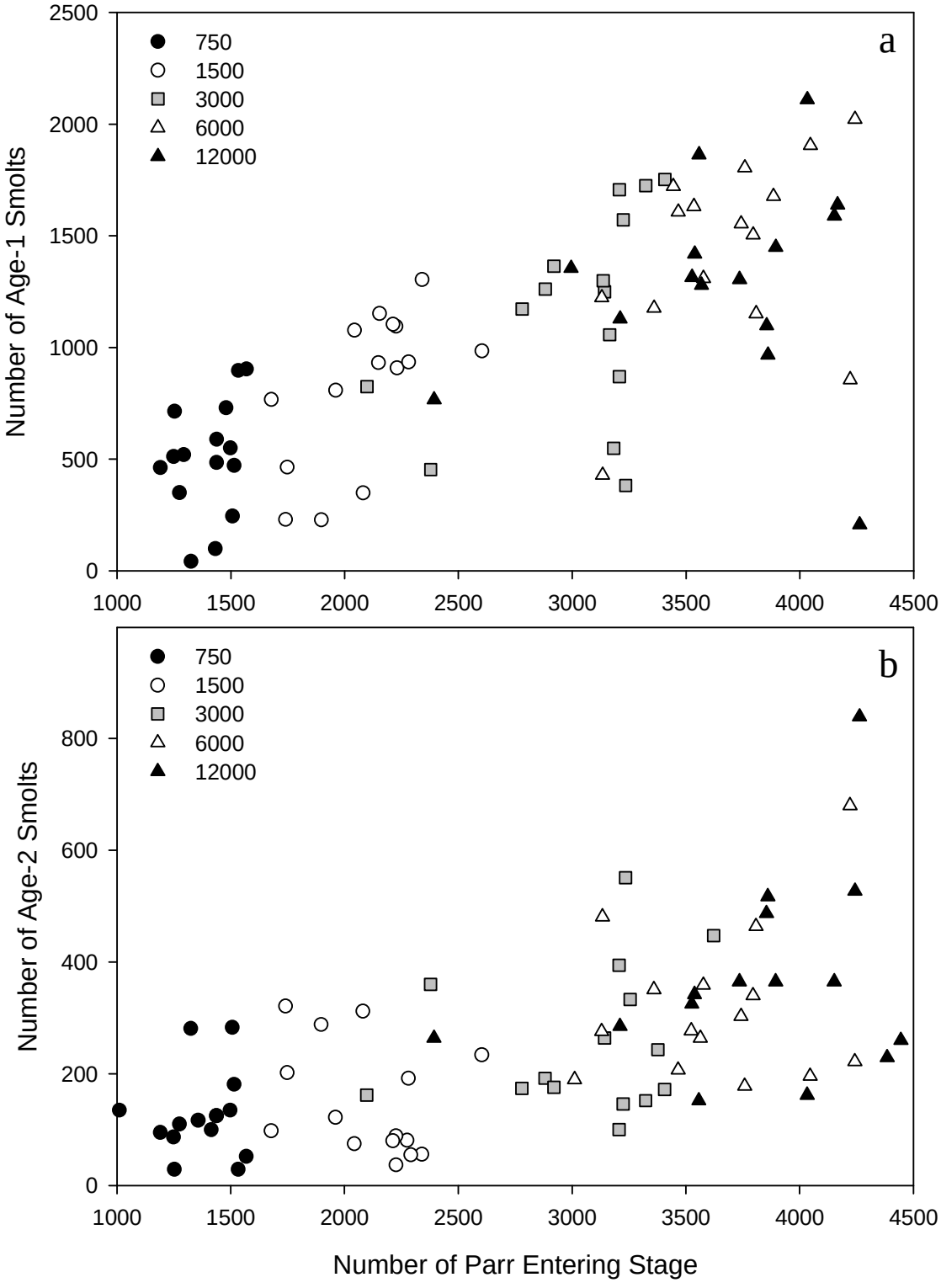

Figure 14. The number of individuals smolting for age-1 (a) and age-2 (b) yearling. The spawning populations were decreased to 750 and 1500, increased to 6000 and 12000, and left at baseline of 3000 female spawners.

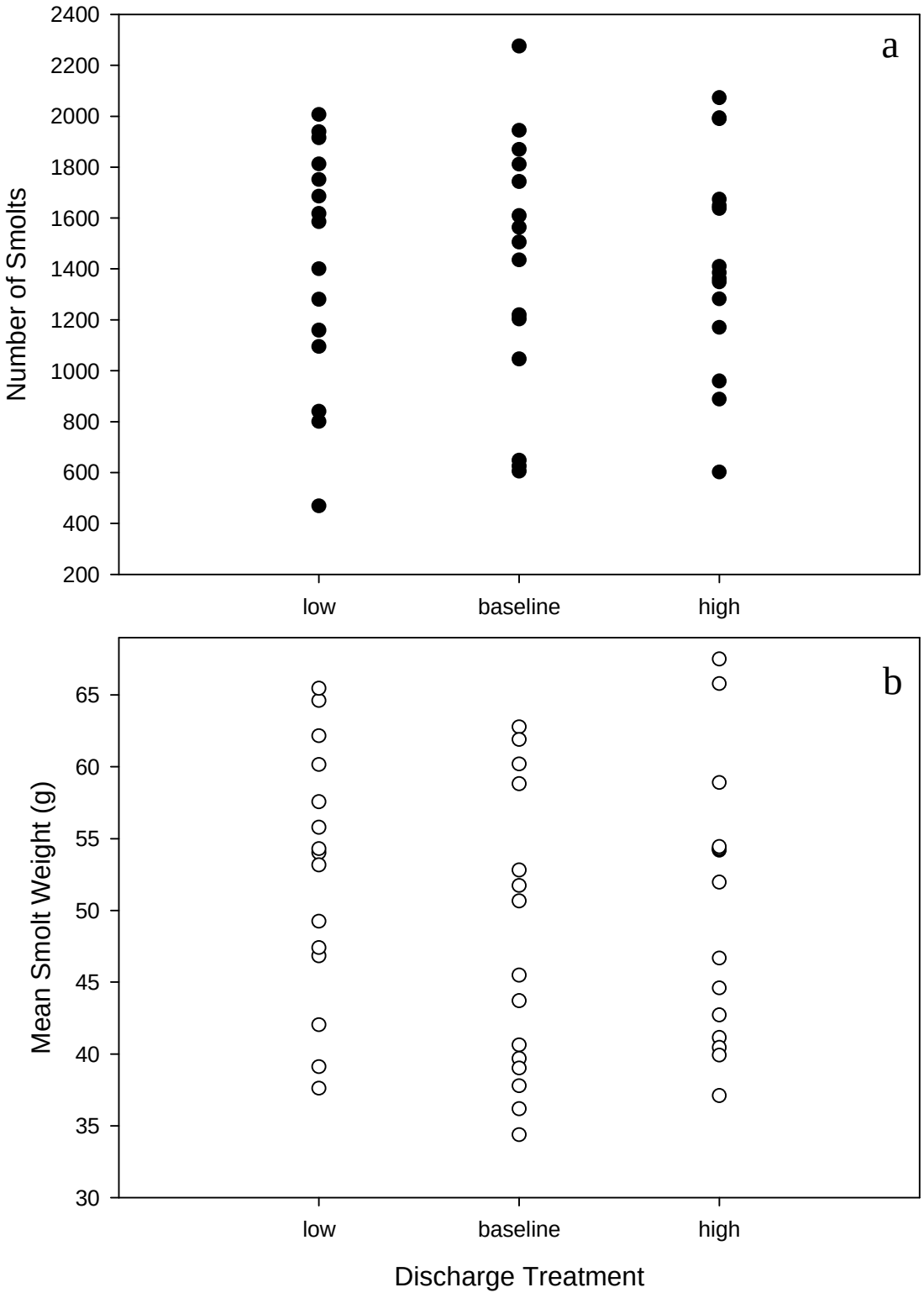

Figure 15. Changes in number of total smolts (a) and mean weights (b) as daily discharge rates are changed from average low and high treatments.

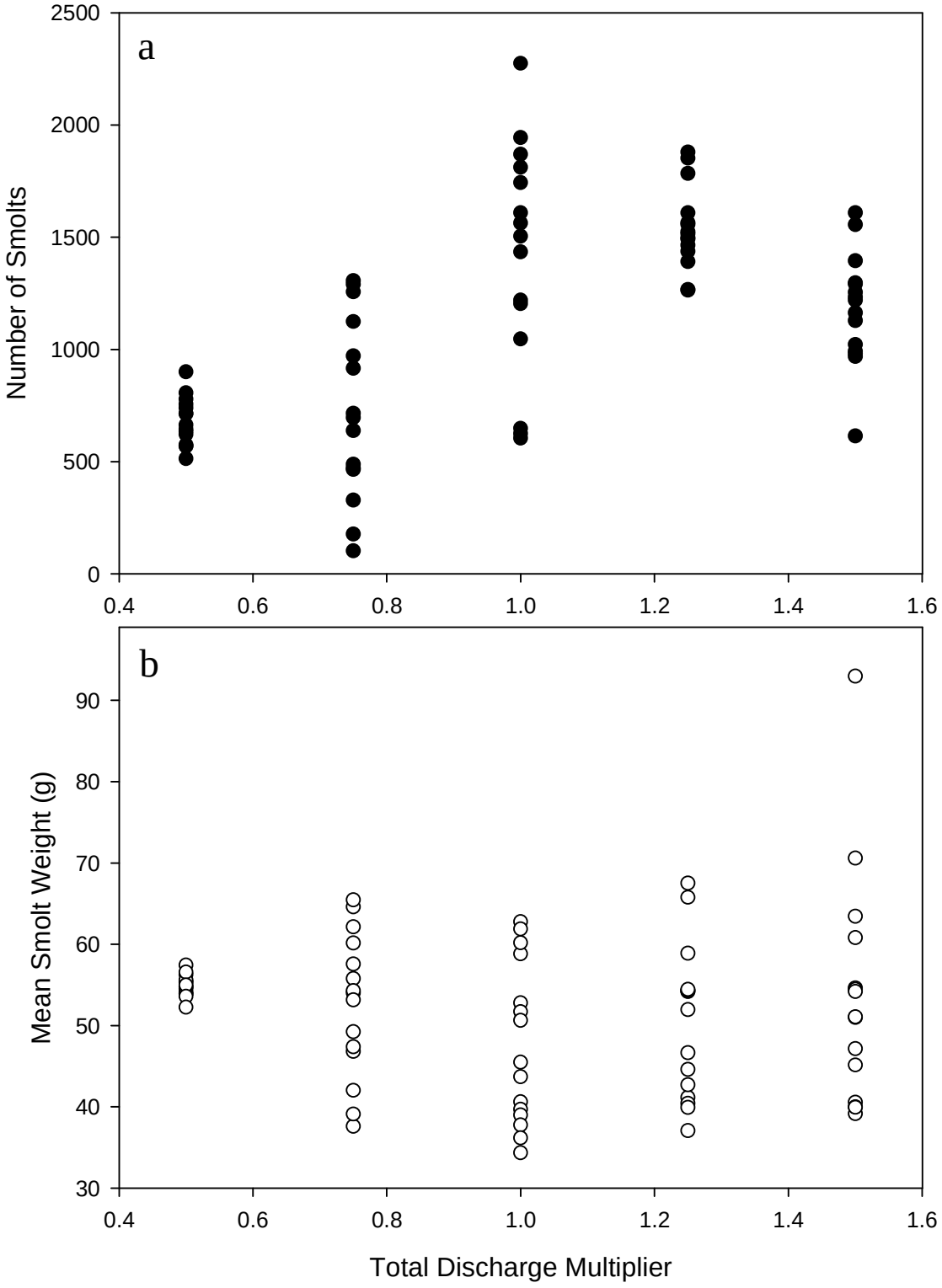

Figure 16. Changes in number of total smolts (a) and mean smolt weight (b) as daily discharge rates are changed with a multiplier of 0.5, 0.75, 1.0 (baseline), 1.25, or 1.5.

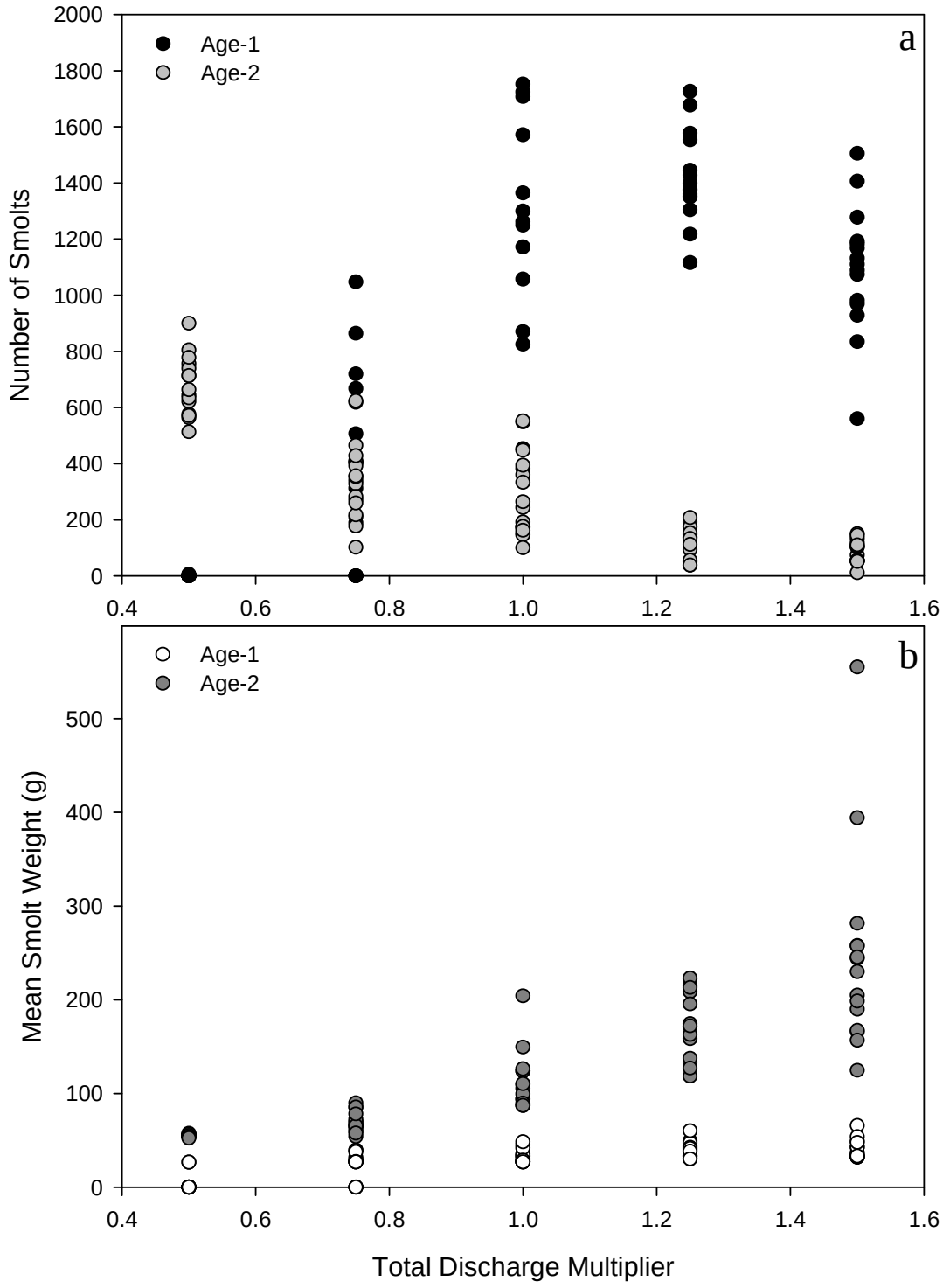

Figure 17. Changes in number of smolts (a) and mean weight (b) as daily discharge rates are changed with the discharge multipliers.

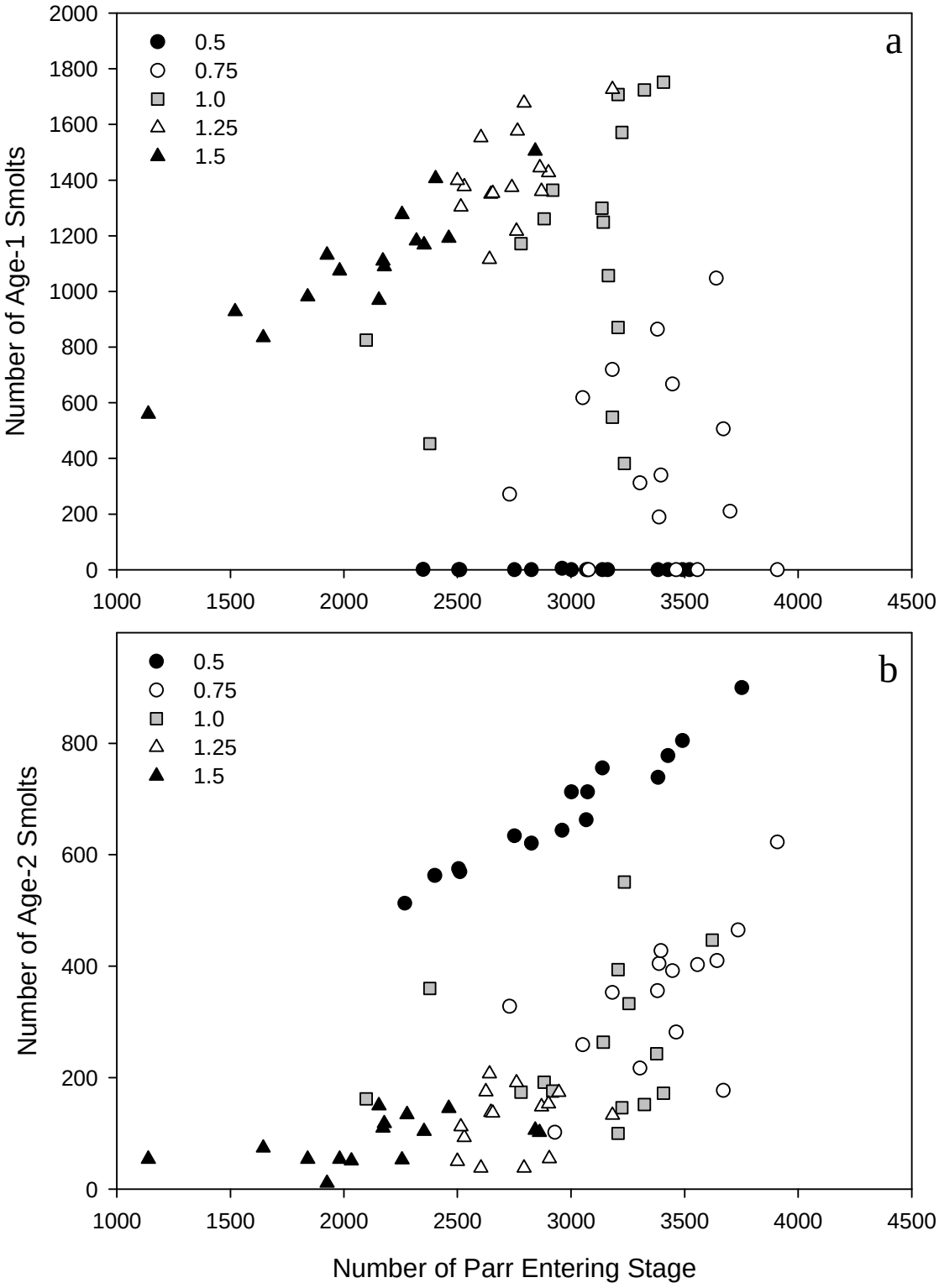

Figure 18. The number of individuals smolting for age-1 (a) and age-2 (b) yearling. The daily discharge rates were changed with 0.5, 0.75, 1.0 (baseline), 1.25, and 1.5 multipliers.

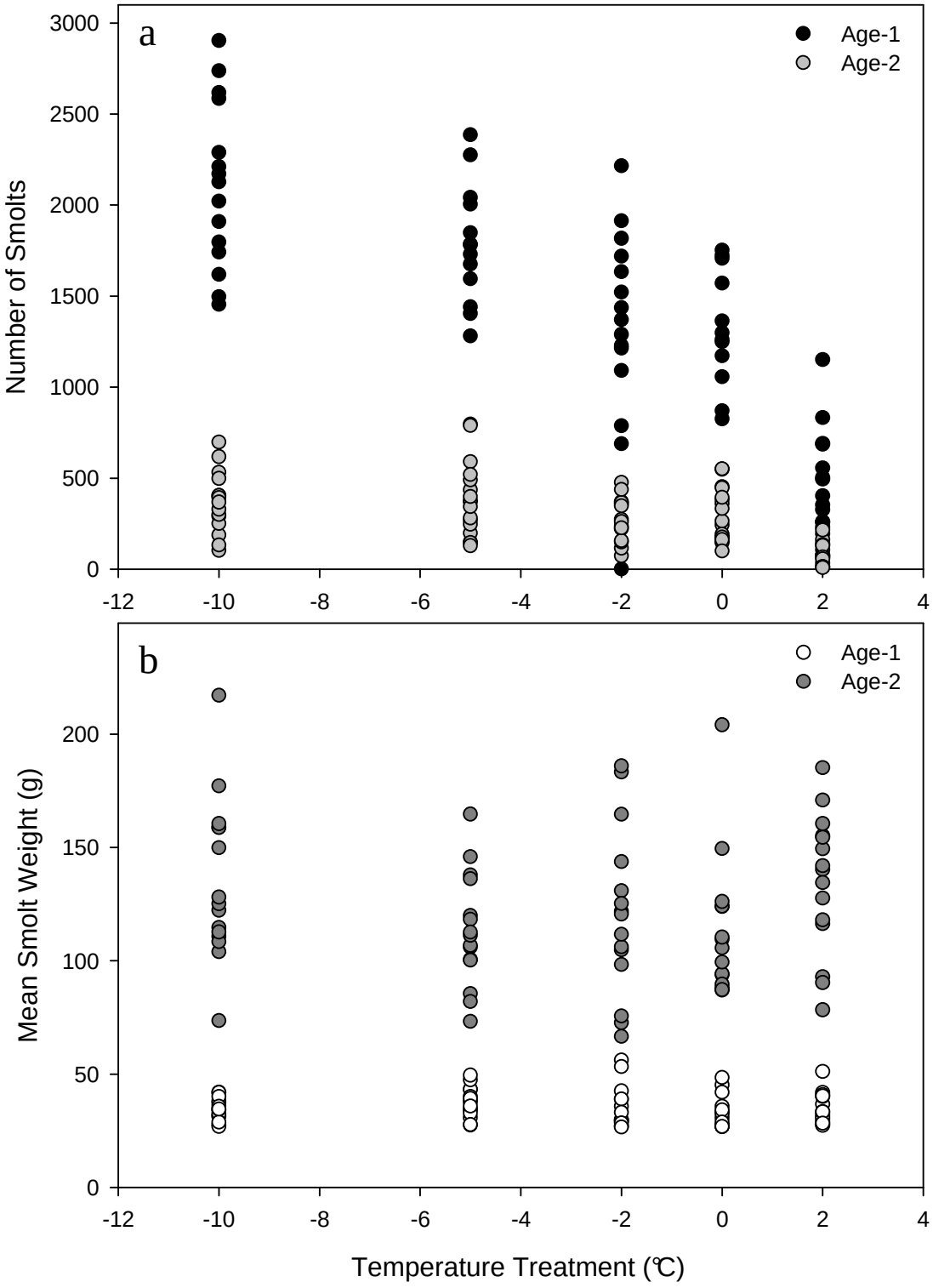

Figure 19. Changes in the number of total smolts (a) and mean smolt weight (b) as mid-summer temperatures increase and decrease from the baseline temperature (0 °C).

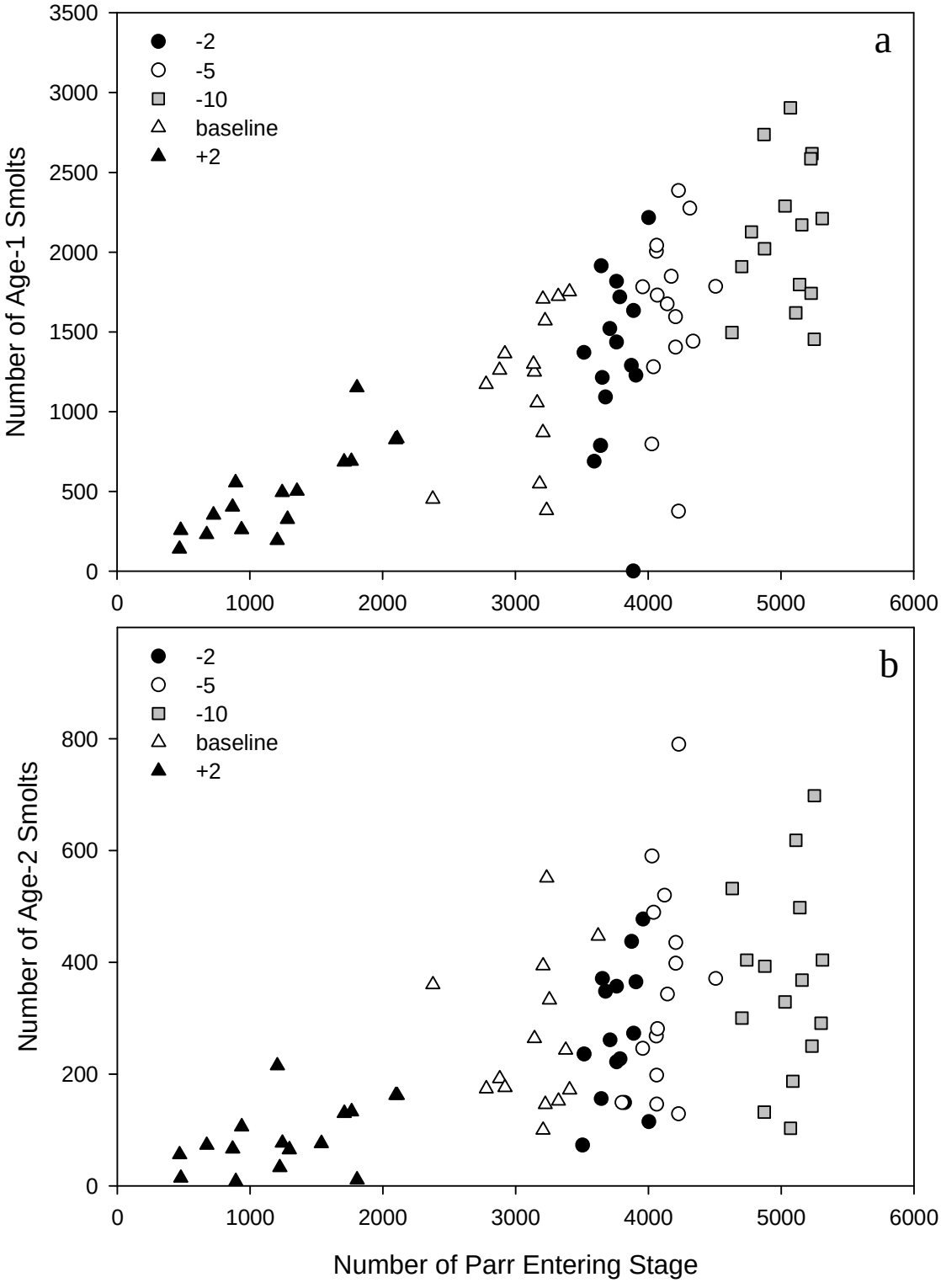

Figure 20. The number of individuals smolting for age-1 (a) and age-2 (b) yearling. The daily temperatures were increased by 2 °C and decreased by 2, 5, and 10 °C.

Appendix A: Individual variation in bioenergetic rates of YOY rainbow trout. Tyler, J. A. and Bolduc, M. B.

Note: Appendix A is work from the first part of my graduate studies. It is not included as a chapter because I was a co-author on the submission of the paper.

Abstract

Studies collecting data on bioenergetic rates in fish typically measure rates on a large number of individuals once and then fit parameter sets to those data sets. Such data commonly have large amounts of variation around the mean which is left unexplained because the study aims to address population- or ecosystem-level questions. Here we aim to address the question of whether individual fish have detectably different rates of maximum consumption and respiration rates or if the process by which these rates are measured introduces the large amounts of variability seen in bioenergetic data sets. We repeatedly measured maximum consumption and respiration rates in individually identified young-of-year (YOY) rainbow trout (*Oncorhynchus mykiss*) over a range of temperatures. In Experiment 1 we measured respiration rates of two size classes of YOY rainbow trout five times at five different temperatures ranging from 9-19 °C. In Experiment 2 we measured respiration and maximum consumption rates of one size class of rainbow trout five times at four different temperatures ranging from 7-19 °C. Results show that individual differences have a significant effect on respiration and maximum consumption rates of YOY rainbow trout. Further analysis of these data shows that the parameters of the weight-dependent component of maximum consumption and respiration rate relationships (intercept, *a*, and exponent, *b*) are closely correlated. Finally, we use these data to develop a new parameter set of the Wisconsin bioenergetics

model of maximum consumption and respiration rates for YOY rainbow trout. These findings may have importance for individual-based models of fish populations which have, to date, not included individual level differences in bioenergetic rates.

Introduction

Bioenergetic models of fish consumption and respiration rates have served the science of fisheries and fish biology well since their inception in the late 1970s (Kitchell et al., 1977; Thorton & Lessem, 1978). Papers in this symposium and the one held in 1992 demonstrate the importance of these models to both basic and applied fisheries science (Brandt & Hartman, 1993). Bioenergetic models have played important roles in a variety of ecological and fisheries analyses including energy transfer among trophic levels (Carpenter, 1988), fish stocking regimes (Rand et al., 1995), habitat suitability for specific species (Roy et al., 2004) and environmental effects on fish populations (Brandt et al., 2002).

The maturation of bioenergetic models of fish growth has played a critical role in the development of individual-based models (IBMs) of fish populations (for reviews see: DeAngelis et al., 1989; Tyler & Rose, 1994; Giske et al., 1998; Werner et al., 2001, Salvanes, 2001). IBMs have not played a similarly important role in the fields of avian or mammalian population ecology in part because of the absence of similarly mature models of growth. IBMs of fish populations have gone to great extents to describe how events may affect individuals differently for example, how population or cohort survivorship may be affected by small differences in size (DeAngelis et al., 1979; Rose & Cowan, 1993), the timing of migrations (Adams & DeAngelis, 1987), and environmental changes

that have seemingly small effects on individual growth (Cowan et al., 1993). One of the consistent themes that arises from various IBM studies is that seemingly insignificant differences in individual fish can have an effect on overall population dynamics; that what happens to the special few individuals that survive to reproduce disproportionally affects the population.

Studies collecting data and developing bioenergetic models of fish growth have shown that endogenous and exogenous factors can significantly affect these rates. Rates differ by species and size class (reviewed in Hanson et al., 1997). Environmental factors such as temperature (Hanson et al., 1997), dissolved oxygen concentration (Buentello et al., 2000; Zhou et al., 2001) and salinity (Wunschel et al., 2005) also affect bioenergetic rates.

Data collected on the key bioenergetic rates of respiration and maximum consumption typically exhibit large amounts of variation around mean values (Rand et al., 1994; Hartman & Brandt, 1995; Myrick & Cech, 1996). Often this variation in the measured rates is considered experimental error because experimenters must handle individual fish considerably to put them into various apparatuses to collect the data. Also, the aim of most studies examining fish bioenergetics is to look for large trends in important rates that determine fish growth. Therefore, these studies have considered variation from the mean to be statistical noise. However, because IBMs of fish populations consistently find that individual differences affect population dynamics and because physiological differences in individuals often is not well depicted in these models (Chambers, 1993), the question of whether variation in bioenergetic rates results from statistical noise or from individual differences deserves attention.

In this paper we aim to examine the question of whether variation from the mean rate of respiration and maximum consumption is in fact statistical noise or if it is a consistent and measurable feature of the individual fish. The experiments in this study consist of repeatedly measuring respiration and maximum consumption rates in young-of-the-year (YOY) rainbow trout (*Oncorhynchus mykiss*) as they grow and at different water temperatures. Because of the data set that we collect here, we address two additional issues. First, the repeated measures of respiration and maximum consumption in YOY rainbow trout allows us to explore correlations that may exist in the parameters that affect the weight component of the models. Both respiration and maximum consumption have a basic equation of the form $rate = aW^b$. We analyze our data to determine if a relationship exists between these two parameters (*a* and *b*). Finally, previous studies have developed bioenergetic models for adult rainbow trout (Rand et al., 1994; Railsback & Rose, 1999), but not for YOY rainbow trout. We use the data collected here to develop a parameter set of the "Wisconsin" bioenergetics model specific for YOY rainbow trout.

Methods

To determine if individual fish consistently differ in their respiration and maximum consumption rates, we conducted two laboratory experiments. The first experiment measured respiration only in two age/size classes of rainbow trout over a range of five temperatures. The second experiment measured respiration and maximum consumption in one size class of rainbow trout over a range of four temperatures. In both

experiments we identified all individual fish with either numbered streamer tags or fin clips.

Fish and Holding Tanks

We obtained young-of-the-year rainbow trout used from the Redwing Trout Hatchery in Montague, MA. Our laboratory holding facility consisted of four 135 L holding tanks in a recirculating system. An overflow pipe in all four tanks allowed for water pumped into each tank to continuously flow into a 750 L head tank. The head tank regulated water temperature, filtered the water, and pumped it back to the four tanks. The tank was equipped with two chillers, a heater, four filters (two fluidized bed filters and two cartridge filters), and two pumps.

Respiration Protocol

Respiration rate experiments were performed on each individual fish multiple times over a range of different temperatures. The fish were allowed to acclimate to the water temperature for at least 24 hours before each trial and fasted for at least 48 hours prior to a trial. Respiration rates were measured as the rate of oxygen consumed by an individual inside a sealed chamber over a timed period. Dissolved oxygen concentration ([DO]) was measured at the beginning and end of each timed period using a YSI 550 DO probe.

The respirometers used in the study were plastic jars with airtight covers that were modified with a bulkhead fitting to provide a quick entry point for the DO probe. During experiments the bulkhead was sealed with multiple layers of parafilm. There were three different size chambers and the size of the fish determined the size of the chamber used:

0.56 L, 2.19 L, or 3.91 L. Tests of this system showed that without fish inside the chamber there was no change in the [DO] readings taken multiple hours apart.

For each measurement we placed one fish inside a respirometer which was then submersed in the head tank and sealed underwater. Timing began when the cover was secure. The period over which oxygen consumption was measured ranged from 30 to 150 min depending on size of the individuals in the chambers, water temperature, and the size of the respirometer used. The starting [DO] was always 100%, as this was the concentration of [DO] in the head tank. The sealed respirometer was then placed in one of the four holding tanks to maintain the chamber temperature throughout the timed period. After the timed period, the respirometer was removed from the holding tank, the parafilm over the bulkhead was punctured, and the [DO] probe was immediately inserted into the respirometer, expunging the water in immediate contact with the parafilm. [DO] measurements were collected as the percent [DO] remaining and were converted to $mg \cdot g^{-1} \cdot d^{-1}$ for statistical analysis and converted to $g \cdot g^{-1} \cdot d^{-1}$ for calibration of the new bioenergetics respiration model.

Maximum Consumption Protocol

The rainbow trout in the consumption experiment were acclimated to the water temperature and fasted the same amount of time as the fish in the respiration protocol. Maximum consumption was measured by the amount of food an individual consumed in two-one hour timed periods that were 16 hours apart. Each fish was placed inside a consumption container, a 5 L bucket with a mesh cover, which was held in one of the four holding tanks to maintain the container's water temperature. A predetermined amount of food (dense culture crumble, Aquatic Ecosystems #FA2) was distributed into

each container. At the end of the hour, the remaining food was filtered (feces were discarded). The food was placed in a drying oven at 63.5 °C for 48 hours. The dried filters were weighed to determine the amount of food not consumed and subtracted from the amount put into the feeding chamber at the start of the timed period. A simple subtraction of the food remaining from the food provided produced the amount of food each individual consumed in that given hour. The amount of food consumed in the two-one hour periods were combined to obtain the $g \cdot g^{-1} \cdot d^{-1}$ of food consumed by each individual.

Experiment 1: Respiration in two size classes

We conducted Experiment 1 from April 2004 to June 2004 in which we collected respiration data from two groups of rainbow trout. The group of small rainbow trout consisted of 15 individuals with a mean weight of 2.05g (standard deviation = 0.36g) at the start of the experiment. The small fish were spawned in the spring of 2004. We divided one of the four holding tanks into three equal sections and placed five small fish in each section and fish in each section were uniquely fin-clipped for identification. The group of large fish included 20 individuals with a mean weight of 61.19g (standard deviation = 12.048g) at the start of the experiment. The large rainbow trout were spawned in the spring of 2003. The 20 large fish were divided among the remaining three tanks and all large individuals received numbered streamer tags (Hallprint corp.) for identification. Before being tagged, the steelhead were anesthetized in a bath with 0.04 $g \cdot L^{-1}$ of MS222 (Schreck & Moyle, 1990).

The respiration experiments were performed on each individual five times at five temperatures: 9, 11, 13, 17, and 19 °C. The sequence of temperature treatments was

randomized. Throughout the study, six small fish and two large fish were lost from various events and their data will not be reported. Results present the data from the nine small and 18 large fish for which we obtained a full set of five respiration measurements at each temperature.

Experiment 2: Respiration and maximum consumption in one size class

Experiment 2 was carried out from November 2004 to February 2005 in which we collected both respiration and maximum consumption rates for a group of 28 rainbow trout. The mean weight of the group at the start of the experiment was 14.45g (standard deviation = 3.016g) and they were spawned in the spring of 2004. The rainbow trout were individually identified with numbered streamer tags using the same procedure as described in Experiment 1. We divided the fish evenly among the four holding tanks. Respiration and maximum consumption measurements were collected five times for each individual at four temperatures: 7, 11, 15, and 19 °C. As with the previous experiment, we randomized the sequence of temperature treatments. Throughout the study, two fish were lost from various events and we do not report their data. Results present the data from the 26 fish for which we have a full set of measurements.

Statistical Analysis

To determine if individuals showed consistent differences in their respiration and maximum consumption rates we analyzed the data from Experiments 1 and 2 with an analysis of variance (ANOVA). In this analysis temperature is treated as a fixed factor, individual as a random factor and weight as a covariate. We treat weight as a covariate because it is intimately linked to individual and because it changes throughout the course of the experiment. We analyze the three groups of rainbow trout (small and large from

Experiment 1 and individuals from Experiment 2) separately for the respiration measurements.

To determine the presence of a relationship between the parameters *a* and *b* in the weight-dependent component of the respiration (*R*) and maximum consumption (C_{max}) equations we first analyzed the data from each individual in Experiment 2 separately. The base equations for these relationships are

$$R = aW^{b} \tag{A- 1}$$

$$C_{\max} = aW^{b} \tag{A- 2}$$

with different values for the *a* and *b* parameters for the two equations. For each individual we regressed the twenty data points of weight against respiration and then against maximum consumption to determine the value of the parameters *a* and *b*. Thus we obtained one pair of parameter values from each individual for respiration and maximum consumption. We then analyzed these values to determine the presence or absence of a relationship between the intercept (*a*) and exponent (*b*) parameters.

The respiration and maximum consumption data from Experiment 2 allow us to also consider if there is a correlation between individuals' respiration and maximum consumption rates. We regressed these values against each other and analyzed for a correlation.

Finally, we fit new parameters for the Wisconsin bioenergetics respiration and maximum consumption models to fit the data that we collected in these experiments. For this we conducted a simple grid search systematically adjusting the values of the five respiration parameters (RA, RB, RQ, RTO and RTM) and the eight maximum consumption parameters (CA, CB, CQ, CTO, CTM, CTL, CK1 and CK4) to obtain the

set that best fit our respiration and maximum consumption data (see Hanson et al. (1997) for definitions of the parameters and equations). We ranked the fit of the predictions to our data based on correlation coefficient (r^2). After selecting the set with the highest correlation, we adjusted the range and resolution of the grid search and repeated. We began with values published by Railsback and Rose (1999) and searched values over a range that was 0.5 and 2.0 times the initial values. We refined the range and resolution of the search until all parameter values changed by less than 0.1% and the correlation between model predictions and our data did not change.

Results

The rainbow trout were weighed regularly throughout the course of the study on the same days as the respiration trials. The weights of rainbow trout generally increased over time in both Experiment 1 (Figure A- 1) and Experiment 2 (Figure A- 2). Of the different temperature treatments used, there were occasional decreases in the mean weight at the beginning of 19 °C trials, but not at any other temperatures. Despite this initial decrease, a net increase in weight was seen at the end of both experiments.

Analysis of individual differences

The analysis of respiration rates for all three groups of rainbow trout (small and large from Experiment 1 and individuals from Experiment 2) showed a significant effect of individuals on respiration rates in all groups (Table A- 1). For all groups the P-value of the effect of individual differences on respiration was ≤ 0.001. The analysis revealed that water temperature also had a statistically significant effect on respiration rates, which is consistent with previous findings (Jobling 1994; Hanson et al 1997). Analysis of

maximum consumption rates from Experiment 2 also showed that the effect of individual differences was significant with P-values similarly low as seen in the analysis of respiration rates (Table A- 2). As expected, water temperature also had a significant effect on maximum consumption.

Analysis of parameter correlation

The analysis of the parameters in the weight-dependent component of the equations for respiration (equation A- 1) and maximum consumption (equation A- 2) showed a tight correlation between the two. The correlation between the intercept (*a*) and exponent (*b*) in the respiration rate data is high ($r^2 = 0.9331$) and a relationship between the two parameters seems visually obvious (Figure A- 3). From Figure A- 3 it may seem that the relationship between the parameters is affected by the one point on the extreme right of the data set, but with that point removed from the regression analysis the correlation between *a* and *b* is still extremely high ($r^2 = 0.9243$). A relationship between the *a* and *b* parameters for maximum consumption (Figure A- 4) also exhibited a high correlation value ($r^2 = 0.9442$) and this data set seems to have no points that may be considered outliers.

The design of the second experiment allowed us to test for a correlation between respiration and maximum consumption rates. Analysis of the data revealed that there is no correlation between the two bioenergetic rates ($r^2 = 0.058$; Figure A- 5). A close examination of the data shows no relationship between respiration and maximum consumption rates at any of the temperatures tested.

New bioenergetics model parameters

The respiration and maximum consumption data allowed us to develop a parameter set for the maximum consumption and respiration rates of the Wisconsin bioenergetics model (Hanson et al. 1997) for YOY rainbow trout (Table A- 3). In creating this parameter set we allowed the data to drive the gridsearch parameter optimization routines that we wrote with one limitation. Experiments of Hokanson et al. (1977) and our own experience holding rainbow trout in the laboratory show that temperatures above about 24 °C result in increased mortality for rainbow trout. Therefore we limited the parameter optimization algorithm such that it would not produce viable maximum consumption and respiration rates at temperatures above 24 °C.

The parameter set that our optimization routines created gives predictions of respiration and maximum consumption rates that differ notably from those created from the parameters developed for adult rainbow trout by Rand et al. (1993) and by Railsback and Rose (1999). The respiration rates predicted by the two adult rainbow trout models typically fall below those that we collected. The relationship between respiration rate and temperature shows adult predictions that are lower than the measured YOY respiration rates and with an optimal temperature that is higher than that which the data support (Figure A- 6). The relationship between respiration rate and fish weight predicted by the adult models is not the same as in the new YOY model or the data, but this difference is not terribly great (Figure A- 7). The maximum consumption rates predicted by the two adult models differ notably from the rates measured for YOY rainbow trout. The relationship between temperature and maximum consumption rates predicted by the two adult models predicts rates that are much higher than those we observed (Figure A- 8).

The same is true for the relationship between weight and maximum consumption (Figure A- 9).

Discussion

The finding of a significant effect of different individuals on respiration and maximum consumption rates in Experiments 1 and 2 represents the most important result in this study. Previous studies measuring bioenergetic rates have shown large amounts of variation in rates (e.g. Hartman and Brandt, 1995; Myrick and Cech, 1996) but focused more on the overall population trend and considered the variability in rates to be statistical noise. Results of the repeated measures of respiration and maximum consumption in these experiments suggest that some of the variability observed in previous studies of bioenergetic rates may result from real differences between individuals rather than statistical noise or experimental error. Because fish weights changed during the course of the study and weight significantly affects bioenergetic rates, we cannot partition the variability in maximum consumption and respiration rates among the factors of individual differences and simple experimental error.

Bioenergetic models of fish growth have played an important role in the development of individual based fish population models (IBMs) (DeAngelis & Gross 1992; Van Winkle et al. 1993 (and many other papers in Transactions of the American Fisheries Society Vol. 122, number 3); Giske et al. 1998). To date, IBMs of fish populations have assumed no difference among individuals' bioenergetic rates because there were no data suggesting the presence of important, detectable differences among individuals of the same species and size class. The results of Experiments 1 and 2 here

show that differences in bioenergetic rates do exist among individual fish of the same species and size class.

Dating back to some of the early models (e.g. DeAngelis et al. 1979), IBMs have consistently shown that in fish populations small differences among individuals can have important effects on population survival and growth rates. Our finding of significant individual differences in the key bioenergetic rates of maximum consumption and respiration suggests that this is a difference that may be important enough to consider including in IBMs of fish populations. The overall effect of variability in bioenergetic rates on the predictions of fish population IBMs is, obviously, uncertain at present. However, because bioenergetic model play a central role in many of these models, the effect of individual variation in these rates should be explored.

Our finding of a significant relationship between the parameters *a* and *b* in the weight dependent components of the respiration and maximum consumption equations (Equations A- 1 and A- 2) was unexpected. For each, increases in the intercept correlated with a decrease in the exponent. Our finding of no correlation between respiration and maximum consumption rates, on the other hand, is unsurprising.

Finally, our data allow us to create a new parameter set for maximum consumption and respiration rate components of the Wisconsin bioenergetics model for YOY rainbow trout. The predictions of the new model differ considerably from those of the models created for adult rainbow trout. The fact that bioenergetic rates differ for adult and YOY stages of a species is a common finding as evidenced by the number of species for which different parameter sets have been developed for adults and YOY (see Hanson et al. 1997). We expect that the parameter set we present here for YOY rainbow trout

bioenergetics will prove useful because the species is widespread and supports valuable fisheries in many areas. We hope that our parameter set allows for more accurate YOY rainbow trout growth or population dynamics models to be developed in the future.

References

Adams, S. M. and DeAngelis, D. L. 1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. Pages 103-117 *in* C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, MA.

Brandt, S. B. and Hartman, K. J. 1993. Innovative approaches with bioenergetics models: applications to fish ecology and management. Transactions of the American Fisheries Society 122: 731-735.

Brandt, S. B. and Mason, D. M. 1994. Landscape approaches for assessing spatial patterns in fish foraging and growth. Page -390 *in* K. Fresh, editor. Theory and application in fish feeding.

Carpenter, S. R. 1988. Complex interactions in lake communities. Springer-Verlag. New York City.

Chambers, R. C. 1993. Phenotypic variability in fish populations and its representation in individual-based models. Transactions of the American Fisheries Society 122: 404-414.

Cowan, J. H., Rose, K. A., Rutherford, E. S., and Houde, E. D. 1993. Individual-based model of young-of-the-year striped bass population dynamics. II. Factors affecting recruitment in the Potomac River, Maryland. Transactions of the American Fisheries Society 122: 439-458.

DeAngelis, D. L., Barnthouse, L. W., Van Winkle, W., and Otto, R. G. 1990. A critical appraisal of population approaches in assessing fish community health. Journal of Great Lakes Research 16: 576-590.

DeAngelis, D. L., Cox, D. K., and Coutant, C. C. 1979. Cannibalism and size dispersal in young-of-the-year largemouth bass: experiment and model. Ecological Modelling 8: 133-148.

DeAngelis, D. L. and Gross, L. J. 1992. Individual-based models and approaches in ecology: populations, communities and ecosystems. Chapman and Hall. New York City, NY, USA.

Giske, J., Huse, G., and Fiksen, O. 1998. Modeling and spatial dynamics of fish. Reviews in fish biology and fisheries 8: 57-91.

Hanson, P. C., Johnson, T. B., Schindler, D. E., and Kitchell, J. F. 1997. Fish bioenergetics 3.0. University of Wisconsin System Sea Grant Institute. Madison.

Hartman, K. J. and Brandt, S. B. 1995. Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. Canadian Journal of Fisheries and Aquatic Sciences 52: 1647-1666.

Hokanson, K. E. F., Kleiner, C. F., and Thorslund, T. W. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile Rainbow Trout, *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34: 639-948.

Jobling, M. 1994. Fish Bioenergetics. Chapman and Hall. New York.

Kitchell, J. F., Stewart, D. J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 34: 1922-1935.

Myrick, C. A. and Cech, J. J. 1996. The effects of elevated rearing temperatures and genetics on trout bioenergetics. Pages 41-47 *in* C. Swanson, P. Young, and D. MacKinlay, editors. Applied environmental physiology of fishes. American Fisheries Society, Bethesda, MD.

Railsback, S. F. and Rose, K. A. 1999. Bioenergetics modeling of stream trout growth: Temperature and food consumption effects. Transactions of the American Fisheries Society 128: 241-256.

Rand, P. S., Stewart, D. J., Lantry, B. F., Rudstam, L. G., Johannsson, O. E., Goyke, A. P., Brandt, S. B., O'Gorman, R., and Eck, G. W. 1995. Effect of lake-wide planktivory by the pelagic prey fish community in Lakes Michigan and Ontario. Canadian Journal of Fisheries and Aquatic Sciences 52: 1546-1563.

Rand, P. S., Lantry, B. F., O'Gorman, R., Owens, R. W., and Stewart, D. J. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978-1990: implications for salmon energetics. Transactions of the American Fisheries Society 123: 519-534.

Rand, P. S., Stewart, D. J., Seelbach, P. W., and Wedge, L. R. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. Transactions of the American Fisheries Society 122: 977-1001.

Rose, K. A. and Cowan, J. H. 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. Transactions of the American Fisheries Society 122: 415-439.

Roy, D., Haffner, G. D., and Brandt, S. B. 2004. Estimating fish production potentials using a temporally explicit model. Ecological Modelling 173: 241-257.

Salvanes, A. G. V. 2001. Review of ecosystem models of fjords; new insights of relevance to fisheries management. Sarsia 86: 441-463.

Schreck, C. B. and Moyle, P. B. 1990. Methods for fish biology. American Fisheries Society. Bethesda, MD.

Thornton, K. W. and Lessem, A. S. 1978. A temperature algorithm for modifying biological rates. Transactions of the American Fisheries Society 107: 284-287.

Tyler, J. A. and Rose, K. A. 1994. Individual variability and spatial heterogeneity in fish population models. Reviews in fish biology and fisheries 4: 91-123.

Van Winkle, W., Rose, K. A., and Chambers, R. C. 1993. Individual-based approach to fish population dynamics: an overview. Transactions of the American Fisheries Society 122: 397-403.

Werner, E. E., Quinlan, J. A., Lough, R. G., and Lynch, D. R. 2001. Spatially-explicit individual based modeling of marine populations: a review of the advances in the 1990s. Sarsia 86: 411-421.

Wuenschel, M. J., Jugovich, A. R., and Hare, J. A. 2005. Metabolic responses of juvenile gray snapper (*Lutjanus griseus*) to temperature and salinity: physiological costs of different environments. Journal of Experimental Marine Biology and Ecology 145: 154.

Zhou, B. S., Wu, R. S. S., Randall, D. J., and Lam, P. K. S. 2001. Bioenergetics and RNA/DNA ratios in common carp (*Cyprinus carpio*) under hypoxia. Journal of Comparative Psychology B-Biochemical Systemic and Environmental Physiology 171: 49-57.

Table A- 1. ANOVA of respiration rates from all three respiration groups.

Group	Source	df	MS	F	P
Experiment 1 (Small)	Weight (covariate)	1	2.71×10^{-6}	0.022	0.882
	Temperature (fixed)	4	0.000	14.752	0.000
	Individual (random)	8	7.59×10^{-6}	1.396	0.001
Experiment 1 (Large)	Weight (covariate)	1	7.61×10^{-6}	0.525	0.469
	Temperature (fixed)	4	0.000	51.493	0.000
	Individual (random)	17	2.32×10^{-5}	16.021	0.000
Experiment 2	Weight (covariate)	1	6.98×10^{-6}	0.026	0.002
	Temperature (fixed)	3	0.000	643.51	0.000
	Individual (random)	25	6.51×10^{-6}	9.386	0.000

Table A- 2. ANOVA of maximum consumption rates.

Source	df	MS	F	P
Weight (covariate)	1	0.020	190.74	0.000
Temperature (fixed)	3	3.25x10-3	35.31	0.000
Individual (random)	25	8.34x10-4	7.86	0.000

Table A- 3. New parameters for maximum consumption and respiration rate equations of the Wisconsin fish bioenergetics model for young-of-year rainbow trout.

Parameter	Value
Consumption	
Equation	3
CA	0.1775
CB	-0.297
CQ	0.06
CTO	14.5
CTM	20.5
CTL	22.0
K1	0.397
K4	0.655
Respiration	
Equation	2
RA	0.01166
RB	-0.0558
RQ	2.792
RTO	18.0
RTM	25.5

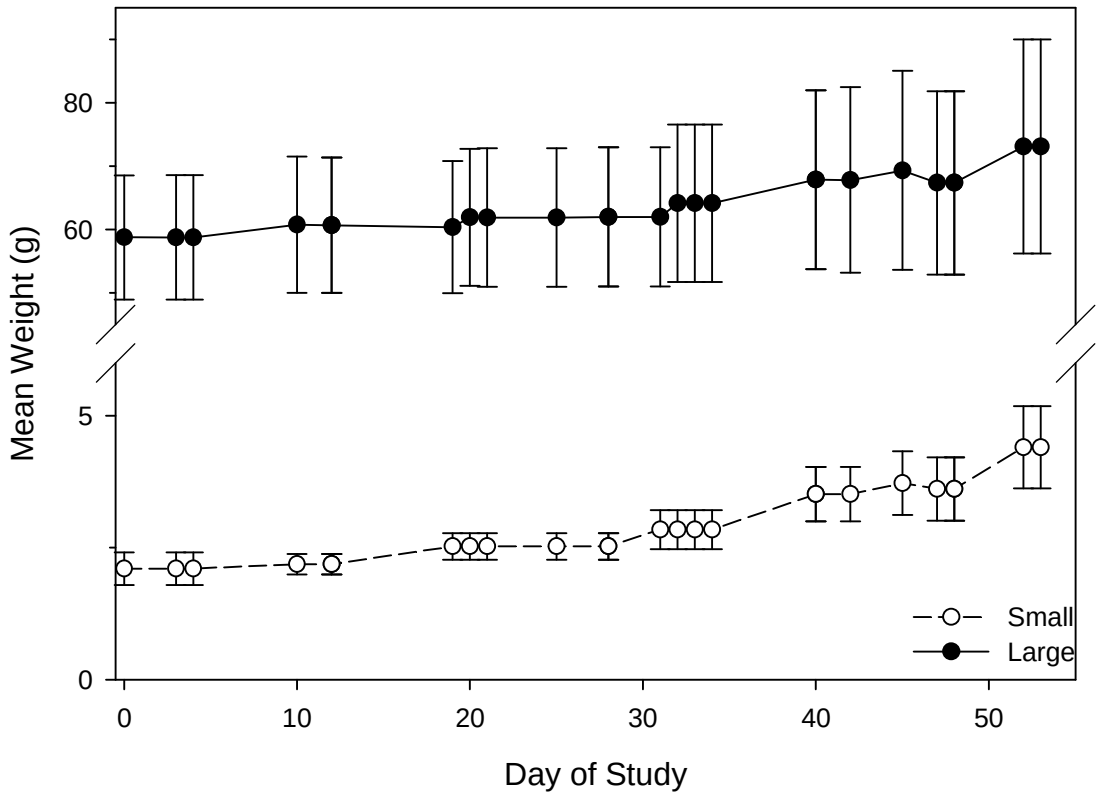

Figure A- 1. Weights of large and small rainbow trout in Experiment 1. Data shown are the mean ±1 standard deviation.

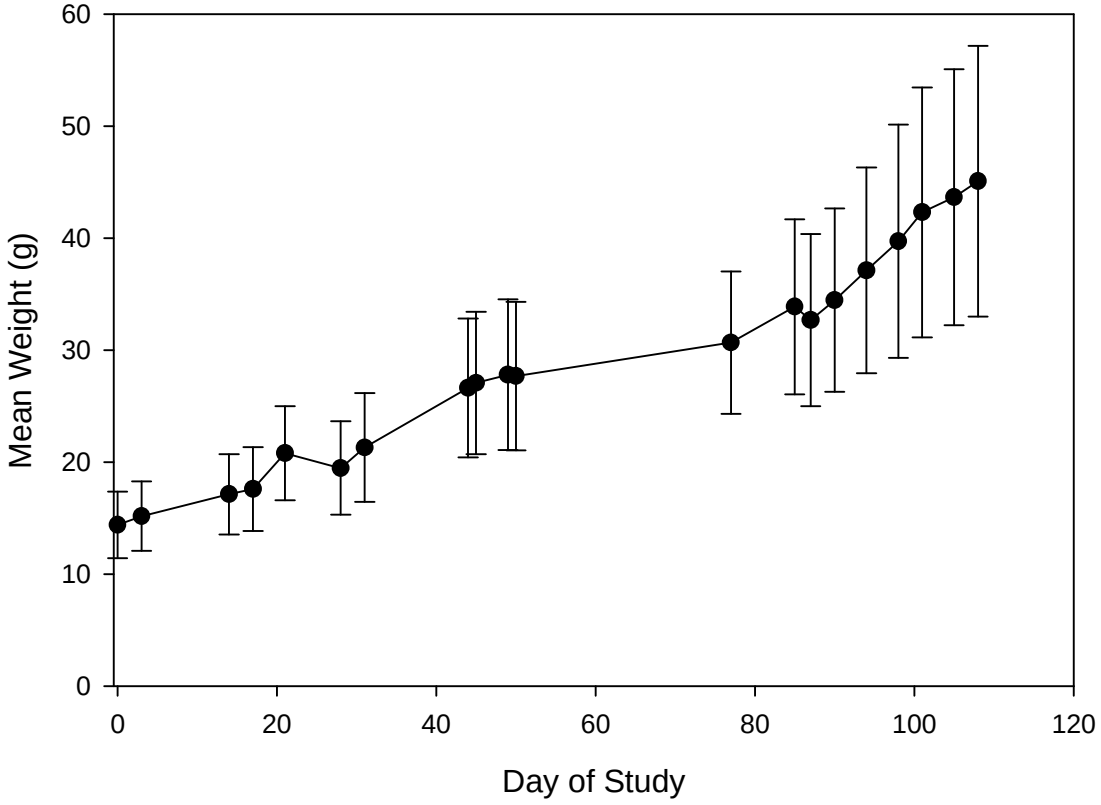

Figure A- 2. Weights of rainbow trout in Experiment 2. Data shown are the mean ±1 standard deviation.

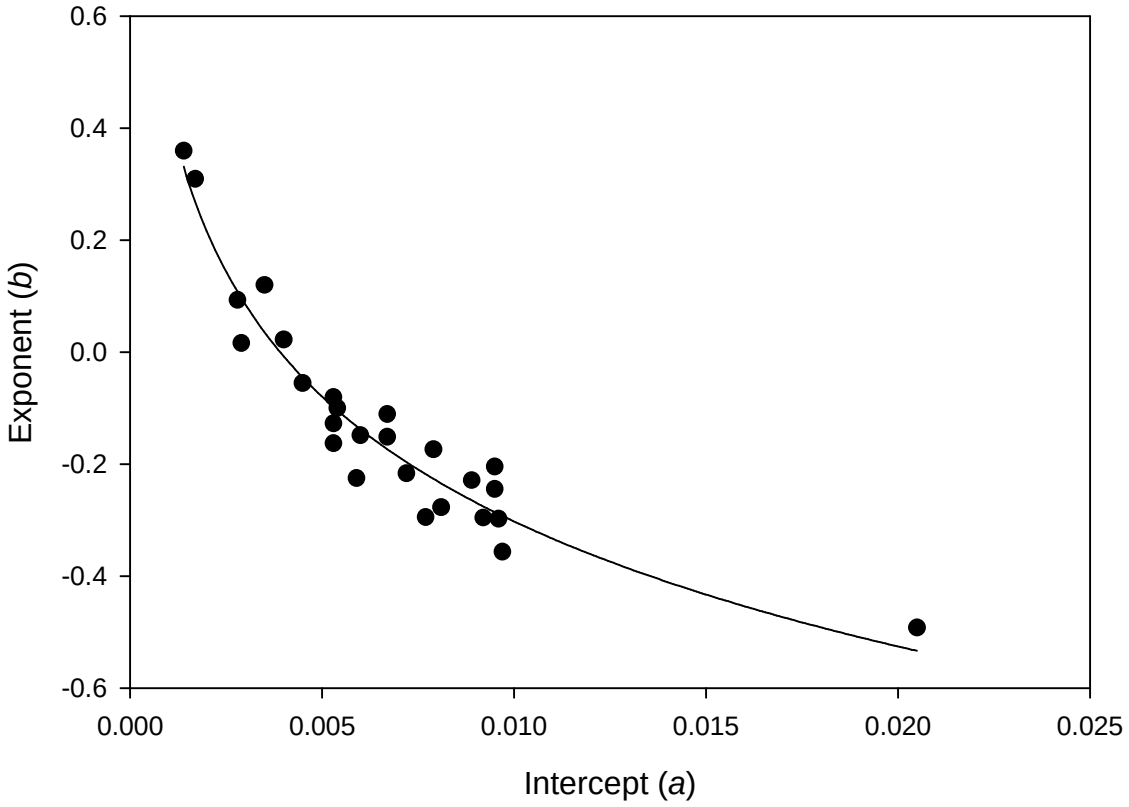

Figure A- 3. Relationship between intercept (*a*) and exponent (*b*) of respiration rates (respiration = aW^b) computed for each individual in Experiment 2, $r^2 = 0.9331$.

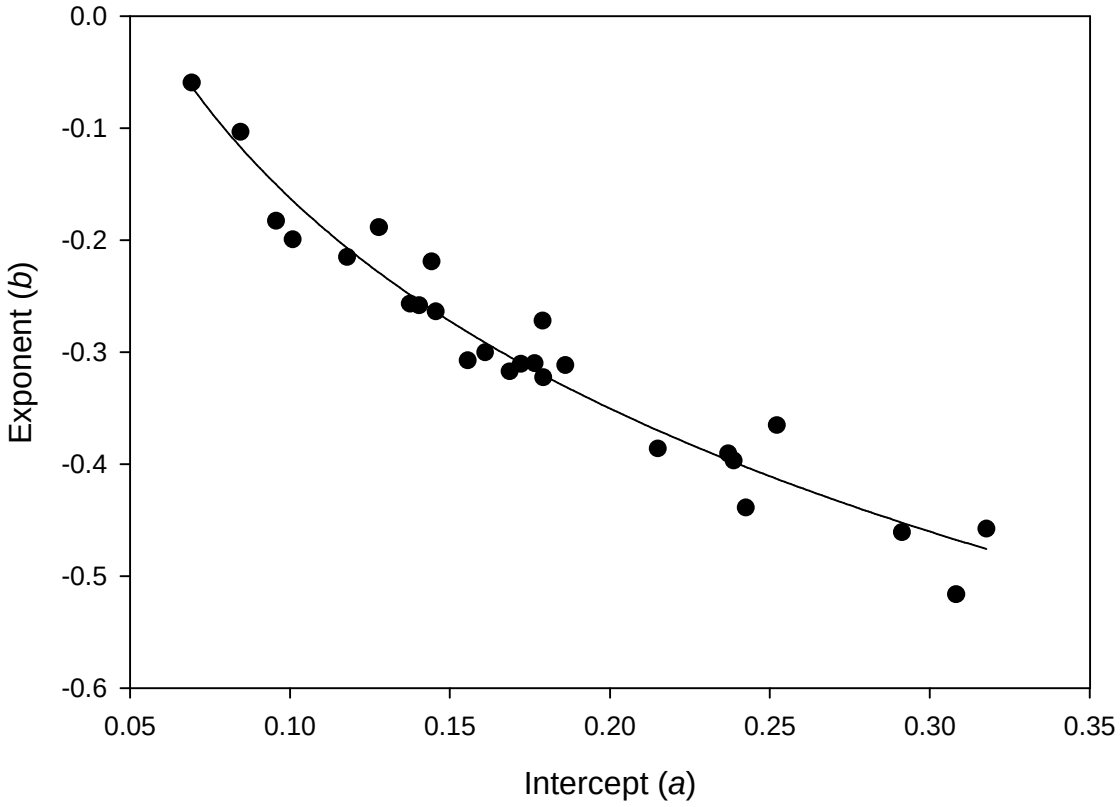

Figure A- 4. Relationship between intercept (*a*) and exponent (*b*) of maximum consumption rates ($C_{max} = aW^b$) computed for each individual in Experiment 2, $r^2 = 0.9442$.

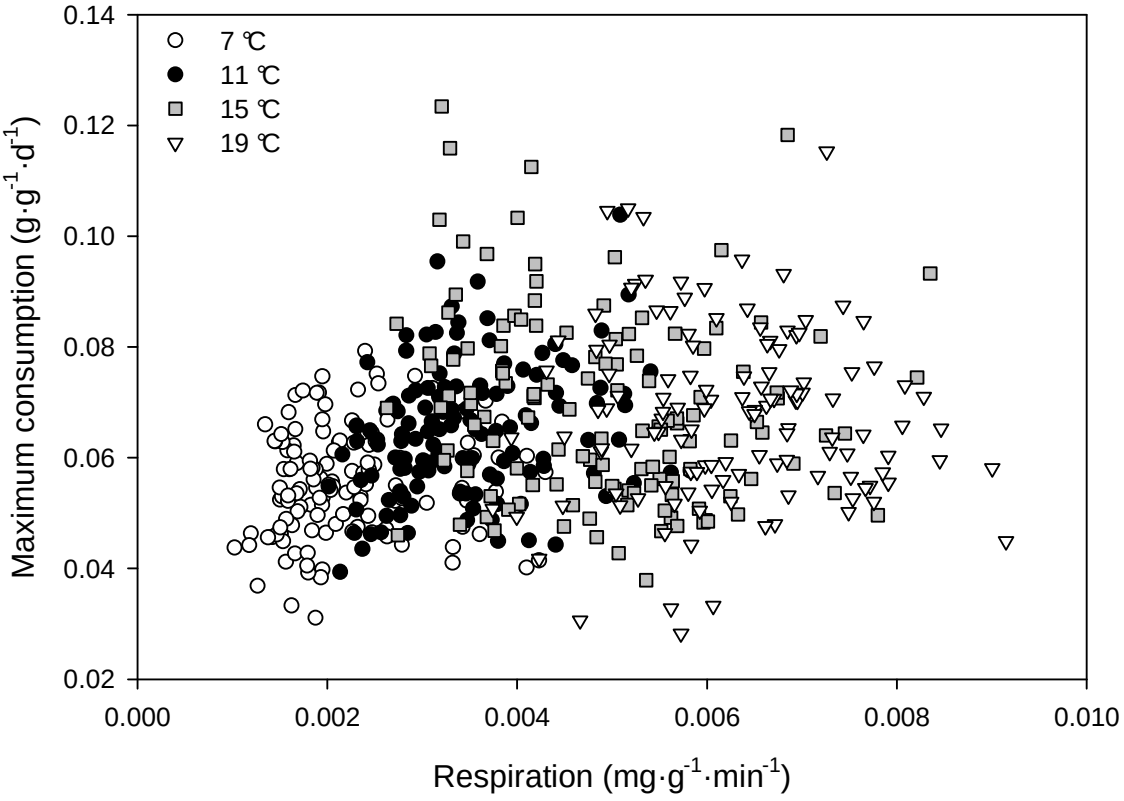

Figure A- 5. Relationship between maximum consumption and respiration rates in Experiment 2.

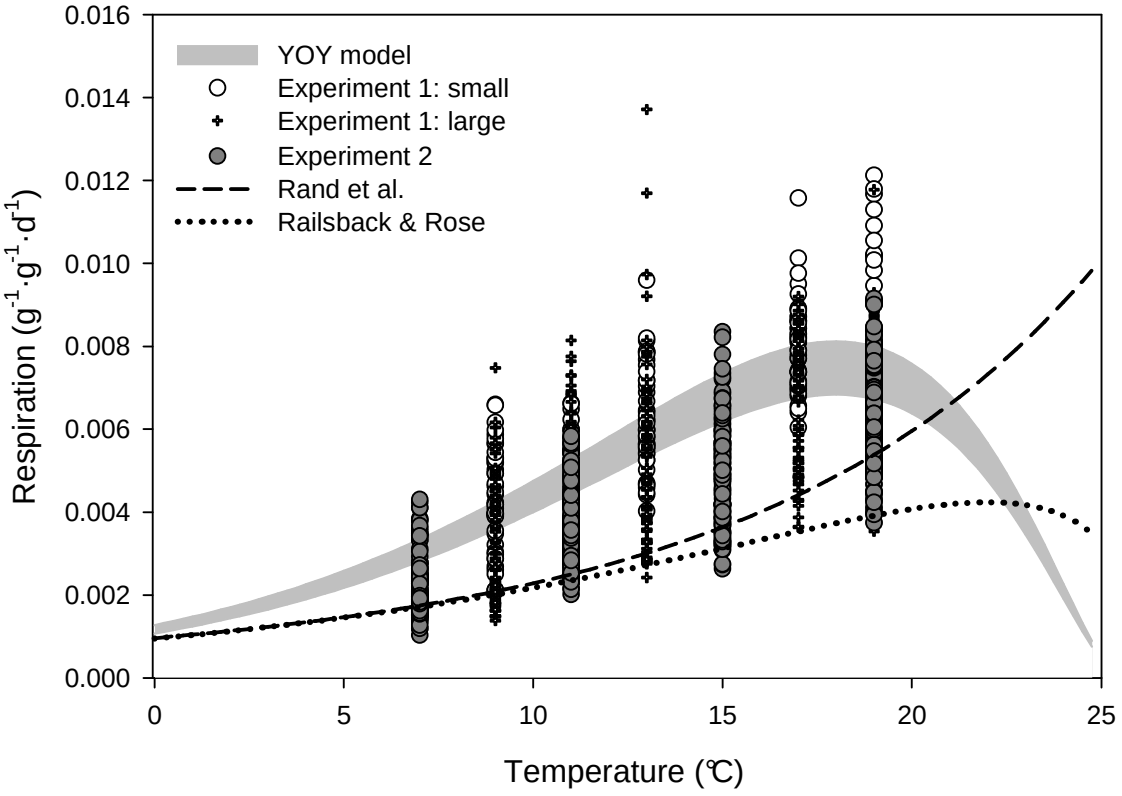

Figure A- 6. Data and model predictions of the relationship between temperature and respiration rates. The gray region represents predictions from the new YOY model over the range of weights set by the mean weight of the small fish and of the large fish in Experiment 1. The predictions from the models by Rand et al. (1993) and Railsback and Rose (1999) use the mean weight of all fish.

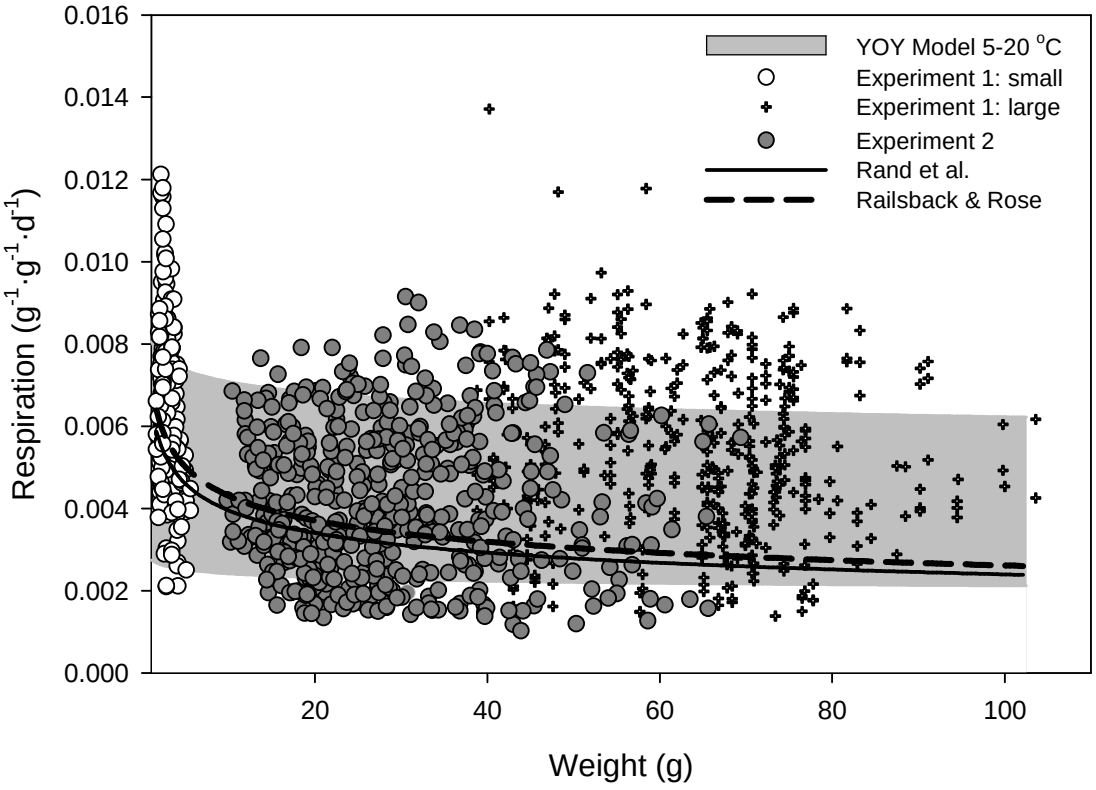

Figure A- 7. Data and model predictions of the relationship between weight and respiration rate. The gray region represents predictions from the new YOY model over the temperature range 5-20 °C. The predictions from the models by Rand et al. (1993) and Railsback and Rose (1999) use a temperature of 15 °C.

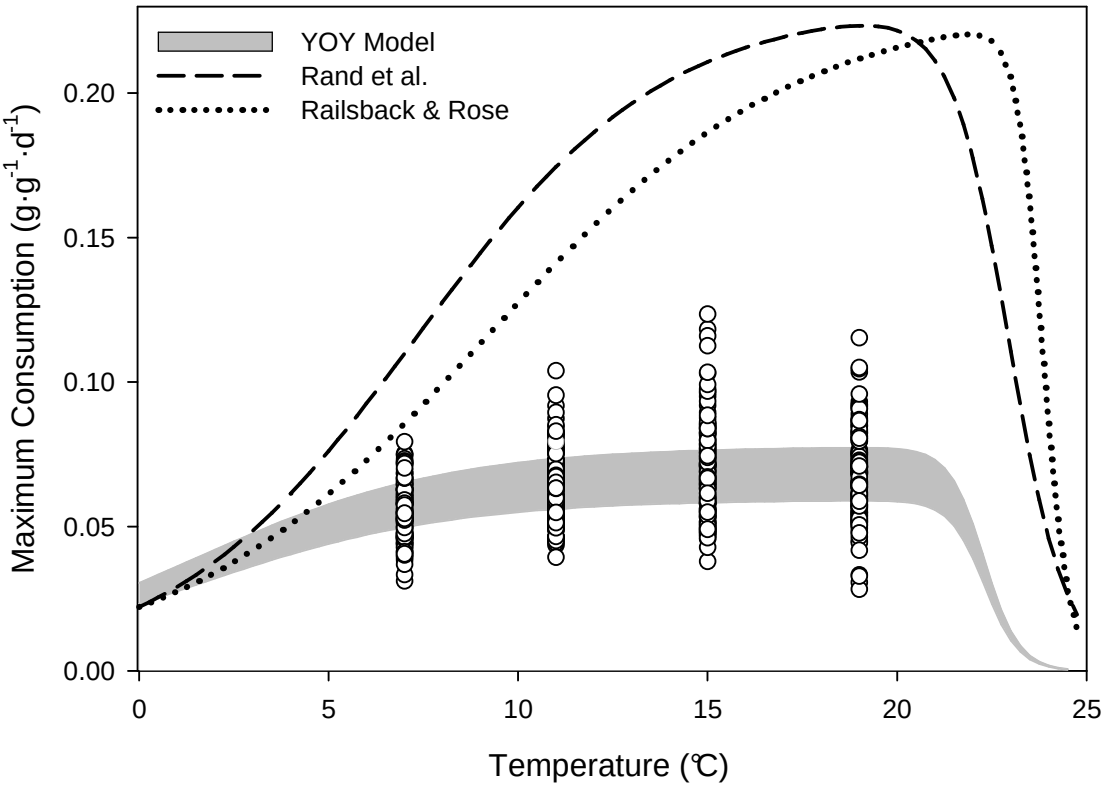

Figure A- 8. Data and model predictions of the relationship between temperature and maximum consumption rate. Model predictions shown include those from the new YOY model at the mean weight of fish in Experiment 2 (solid line) ±1 SD (gray) and those from models by Rand et al. (1993) and by Railsback and Rose (1999) for only the mean weight of fish in Experiment 2.

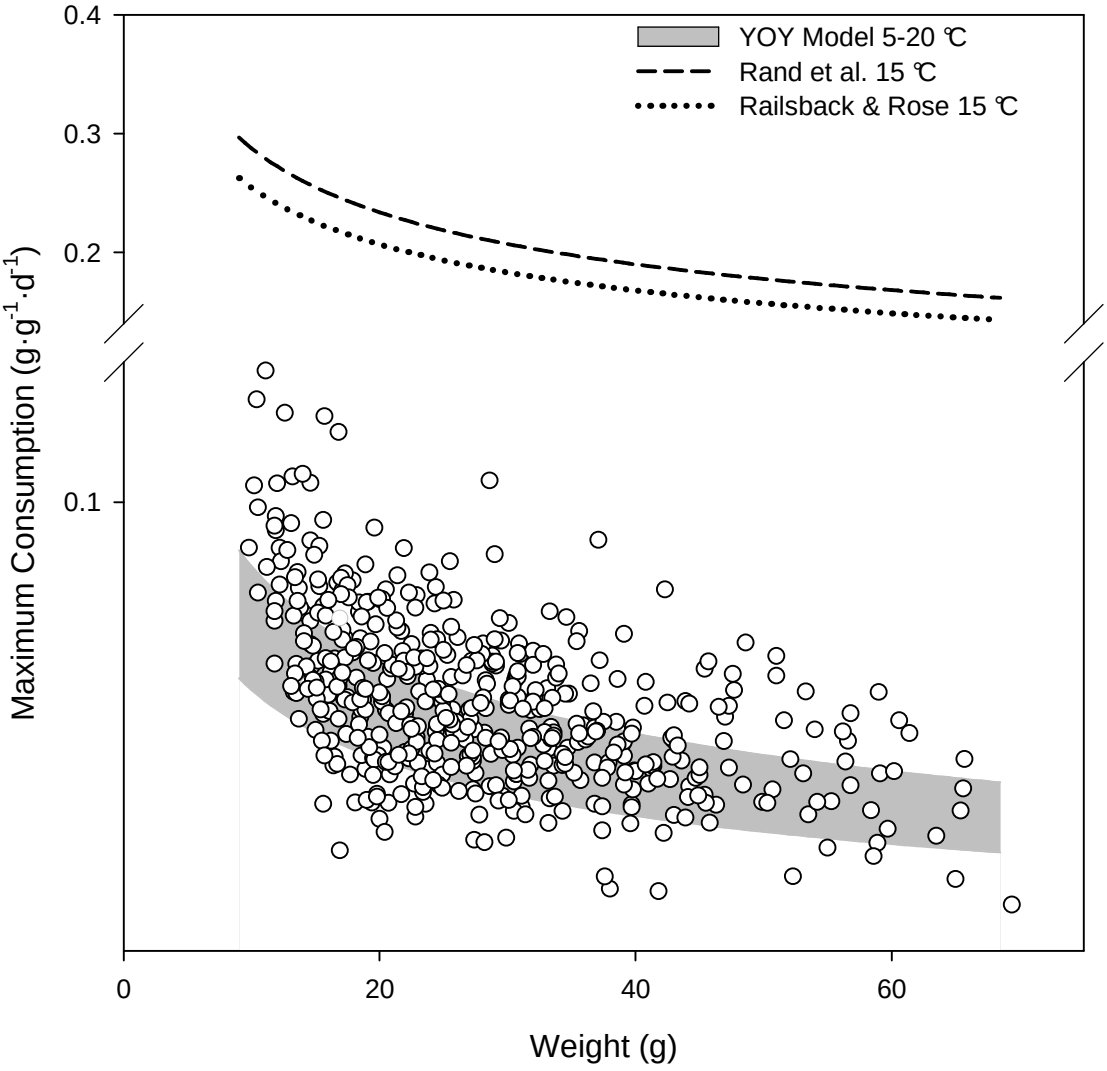

Figure A- 9. Data and model predictions of the relationship between weight and maximum consumption rate. The gray region represents predictions from the new YOY model over the temperature range 5-20 °C. The predictions from the models by Rand et al. (1993) and Railsback and Rose (1999) use a temperature of 15 °C.